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Cover photo: Two pseudoscorpions (Chernetidae) hanging onto the underside of a fly (Muscoidea) in eastern Massachusetts. This is an example of phoresy, the term for one organism attaching to another as a means of transportation. Photo by Joe Warfel.

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The systematics of the pseudoscorpion family Ideoroncidae (Pseudoscorpiones: Neobisioidea) in the New World

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Abstract. A review of the pseudoscorpion family Ideoroncidae in North and South America has revealed seven genera and 43 species. The genus *Albiorix* occurs in xeric environments in western USA and in Mexico, with two outlying species in Chile and Argentina. It includes 18 species, including five new species from Mexico (*A. meraculus*, *A. minor*, *A. oaxaca*, *A. puebla* and *A. rosario*), and three from USA (*A. gertschi*, *A. sarahae* and *A. vigintus*). *Albiorix bolivari* is treated as a junior synonym of *A. retrodentatus*. The genus *Ideoroncus* has nine species and is endemic to southern Brazil and Paraguay. *Pseudalbiorix* has four species and occurs in Central America and western Cuba. *Typhloroncus* has six species from Mexico and U.S. Virgin Islands, including the new species *T. planodentatus* from Mexico. *Xorilbia* has three species and occurs in the Amazonian rainforest ecosystems of northern Brazil and southern Venezuela. Two new genera are described: *Mahnertius* Harvey & Muchmore for the new species *M. stipodentatus* (type species) and *M. hadrodentatus*, both from Colombia; and *Muchmoreus* Harvey for the new species *M. ignotus* (type species) from Mexico. Several keys are provided, including one to separate the New World genera, and others to distinguish the species of each genus (apart from the monotypic *Muchmoreus*). The post-embryonic development of New World ideoroncids is reviewed, particularly the trichobothrial patterns of nymphs and adults.

Keywords: Pseudoscorpions, taxonomy, morphology, new species, new genera, post-embryonic development

The pseudoscorpion family Ideoroncidae was first recognized and named by Chamberlin (1930), who included two subfamilies and four genera: the subfamily Ideoroncinae for the genera *Ideoroncus* Balzan 1887 from South America, *Albiorix* Chamberlin 1930 from North America, and *Dhanus* Chamberlin 1930 and *Shravana* Chamberlin 1930 from southeast Asia, and the subfamily Bochicinae for the monotypic *Bochica* Chamberlin 1930 from the West Indies. Beier (1931) added the genera *Negroroncus* Beier 1931 from east Africa and *Dinoroncus* Beier 1931 from Chile, each represented by single species. Beier (1932b) recognized both subfamilies but also added the subfamily Hyinae, which Chamberlin (1930) had previously proposed as a distinct family. Beier (1931, 1932b) added the Bolivian genus *Mirobisium* Beier 1931 to Bochicinae, but this genus was later recognized as a close relative of *Gymnobisium* Beier 1931, and both genera, along with *Vachonobisium* Vitali-di Castri 1963, were treated as members of the family Vachoniidae by Vitali-di Castri (1963) and of the Gymnobisiidae by Beier (1964) and Muchmore (1972). Further genera of Ideoroncinae were added from various tropical regions of the world. Redikorzev (1938) described *Nhatrangia* Redikorzev 1938 from southeast Asia. Beier (1955) and Mahnert (1981a) recognized new African genera, *Nannoroncus* Beier 1955 and *Afroroncus* Mahnert 1981, respectively, whilst Muchmore (1979, 1982b, 1986) described various species of *Typhloroncus* Muchmore 1979 from the Caribbean region. Most recently, Harvey et al. (2007) recognized *Pseudalbiorix* Harvey, Barba, Muchmore and Peréz, 2007 from Central America.

In the meantime, the Hyinae was reinstated as a distinct family by Chamberlin (1946) and *Bochica* was placed in its own family, Bochicidae, by Muchmore (1982a). Bochicidae was later expanded with the inclusion of the previously separate family Vachoniidae by 1992) and 1998). The removal of these various genera from the Ideoroncidae to other families has left a tightly-knit group of genera within Ideoroncidae characterized by the presence of supernumerary trichobothria on the fixed and movable fingers of the pedipalpal chelae, and the median maxillary lyrifissure being located sub-basally on the pedipalpal coxa (1992). The family currently contains 59 species in 10 genera (Harvey 2013) and occurs throughout most tropical and sub-tropical regions of the world with the exception of Australia and West Africa (Harvey 2013).

Of the five named New World genera of the Ideoroncidae, *Ideoroncus* is restricted to Brazil and Paraguay, *Albiorix* is found in Mexico and southwestern U.S.A., as well as Argentina and Chile, *Pseudalbiorix* is found in Cuba, southern Mexico, Belize and Guatemala, *Typhloroncus* occurs in the Virgin Islands and Mexico, and *Xorilbia* is restricted to the Amazonian region (Harvey 2013). Although many New World species have been well described and illustrated, some of the older species are poorly known. In particular the identity of some members of the genus *Albiorix* is difficult to verify based upon the original descriptions. Our attempts to consistently identify new specimens of *Albiorix* from the USA and Mexico based upon the keys presented by Chamberlin (1930) and Hoff (1945) proved ineffective, mainly due to the poor understanding of intraspecific variation within the genus. We have examined numerous specimens as part of a review of the group and here present the results of that study. We present illustrated redescriptions of most of the older species of *Albiorix*, and describe several new

species of *Albiorix* as well as the first species of *Typhloroncus* with eyes. We have also found three new species from Mexico and Colombia that could not be placed in any existing genus, for which we erect two new genera.

METHODS

The specimens examined during this study are deposited in the American Museum of Natural History, New York, New York, USA (AMNH); California Academy of Sciences, San Francisco, California, USA (CAS); Colección Nacional de Arácnidos, Instituto de Biología, Universidad Nacional Autónoma de México, Cuidad de México, Distrito Federal, México (CNAN); Florida State Collection of Arthropods, Gainesville, Florida, USA (FSCA); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (MCZ); Museo Zoologio di Università degli Studi di Napoli, Portici, Italy (MZUN); Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA (PMNH); Bohart Museum of Entomology, University of California, Davis, California, USA (UCDC); University of California, Riverside, California, USA (UCRC) and the Western Australian Museum, Perth, Australia (WAM).

Most specimens newly examined for this study were slide-mounted by the second author (W.B. Muchmore) in Canada balsam, generally using the methods described by Hoff (1949). Other specimens were examined by the senior author (M.S. Harvey) by preparing temporary slide mounts by immersing the specimen in 75% lactic acid at room temperature for one to several days, and mounting them on microscope slides with 10 or 12 mm coverslips supported by small sections of 0.25 mm or 0.50 mm diameter nylon fishing line. Specimens were examined with a Leica MZ16 dissecting microscope, Leica DM2500 or Olympus BH–2 compound microscopes, and illustrated with the aid of a drawing tube. Measurements were taken at the highest possible magnification using an ocular graticule. After study the specimens were returned to 75% ethanol with the dissected portions and placed in 12 × 3 mm glass genitalia mierovials (BioQuip Products, Inc.).

The setae of the carapace are shown as a solid line if present, but depicted with a dashed line if the seta was missing from the specimen. Other small dots depicted in the illustrations are small pores, and not setal areolae.

The genera and species treated in this monograph are arranged alphabetically. Terminology and mensuration largely follow Chamberlin (1931), with the exception of the nomenclature of the pedipalps, legs and with some minor modifications to the terminology of the trichobothria (Harvey 1992), chelicera (Harvey & Edward 2007; Judson 2007) and faees of the appendages (Harvey et al. 2012). The notation of the supernumerary trichobothria follows Mahnert (1984a).

Coordinates for the collection localities were calculated using Google Earth or obtained from various other on-line resources. The spellings of the Mexican place names generally follow Reddell (1981).

SYSTEMATICS

Family Ideoroncidae Chamberlin 1930

Ideoroncidae Chamberlin 1930:42; Chamberlin 1931:220; Beier 1932a:166; Beier 1932b:183; Roewer 1937:254; Hoff 1956:25; Murthy and Ananthakrishnan 1977:25–26; Muchmore 1982a: 97–98; Harvey 1991:315; Harvey 1992:1408; Harvey 2013:unpaginated.

Ideoroncinae Chamberlin 1930:44; Chamberlin 1931:220; Beier 1932a:170; Roewer 1937:256; Hoff 1956:25.

Diagnosis.—Species of Ideoroncidae can be readily distinguished from all other pseudoscorpions by the presence of multiple trichobothria on the chelae, with 19 or more on the chelal hand and fixed finger and 10 or more on the movable chelal finger (e.g., Figs. 4, 27B, 31C). Adults of most other pseudoscorpion families have a maximum of 8 trichobothria on the fixed finger and chelal hand, and 4 trichobothria on the movable chelal finger. The only exception is within the family Menthidae, whose members have a pattern of 11 + 4. Ideoroncids can also be easily recognized by the position of the median maxillary lyrifissure, which is situated sub-basally on the pedipalpal maxilla (Fig. 7A) (it is sub-medial or sub-distal in other families) and the deeply divided median genital sac in males (Fig. 6B) (it is usually entire in the majority of families).

Description.—*Adults:* setae: long, straight and acicular.

Chelicera (Figs. 7A, 7B, 28B, 29C): hand with 6–9 setae; movable finger with 1 long seta; rallum of 4 thickened blades; galea simple, long and slender.

Pedipalp: fixed chelal finger and hand with 19–31 trichobothria, movable chelal finger with 10–14 trichobothria (e.g., Figs. 5, 28C, 31C). Venom apparatus present in both chelal fingers, venom ducts long (e.g., Figs. 8C, 24B, 29D, 31E).

Carapace: with 2 bulging eyes (e.g., Figs. 17A, 21A, 27A, 29A), or in some species absent (Fig. 8A).

Coxal region (Fig. 6A): manducatory process with 2 long distal setae; median maxillary lyrifissure present and sub-basally situated.

Legs (Figs. 7F, 7G): femur I and II without basal swelling; femora I and II with primary slit sensillum directed transversely; femur I much longer than patella I; suture line between femur IV and patella IV transverse; metatarsus shorter than tarsus; without sub-ungual spine; claws slender and simple.

Abdomen: pleural membrane longitudinally striate (Fig. 6F); spiracles simple, with spiracular helix (Fig. 6E); setae of anterior genital operculum (sternite II) of female very small (Fig. 6D).

Genitalia: male median genital sac bipartite (Fig. 6B); female with large gonosac covered with scattered pores (Fig. 6C).

Post-embryonic development.—Mahnert (1979, 1981a, 1981b, 1984a), Harvey (1992) and Harvey et al. (2007) presented data on the trichobothrial patterns occurring in the nymphs of various species of Ideoroncidae. Mahnert (1979, 1984a) provided complete post-embryonic sequences (i.e., protonymph, deutonymph, tritonymph and adult) for a single New World species (*Ideoroncus setosus*) and partial data on one or two nymphal stages in addition to the adult (*I. divisus*, *I. lenkoi*, *I. paranensis* and *Albiorix arboricola*). Harvey et al. (2007) provided data for *Pseudalbiorix reddelli* and partial data for *P. armasi* (tritonymph) and *P. veracruzensis* (tritonymph). We now add complete data for *A. chilensis* (Fig. 4), and partial data for *A. anophthalmus* (deutonymph), *A. conodentatus* (tritonymph and deutonymph), *A. meraculus* (tritonymph), *A. mexicanus* (tritonymph), *A. parvidentatus* (tritonymph), *A. retrodentatus* (tritonymph) and *Muchmoreus ignotus* (tritonymph) (Table 1). As in all pseudoscorpions

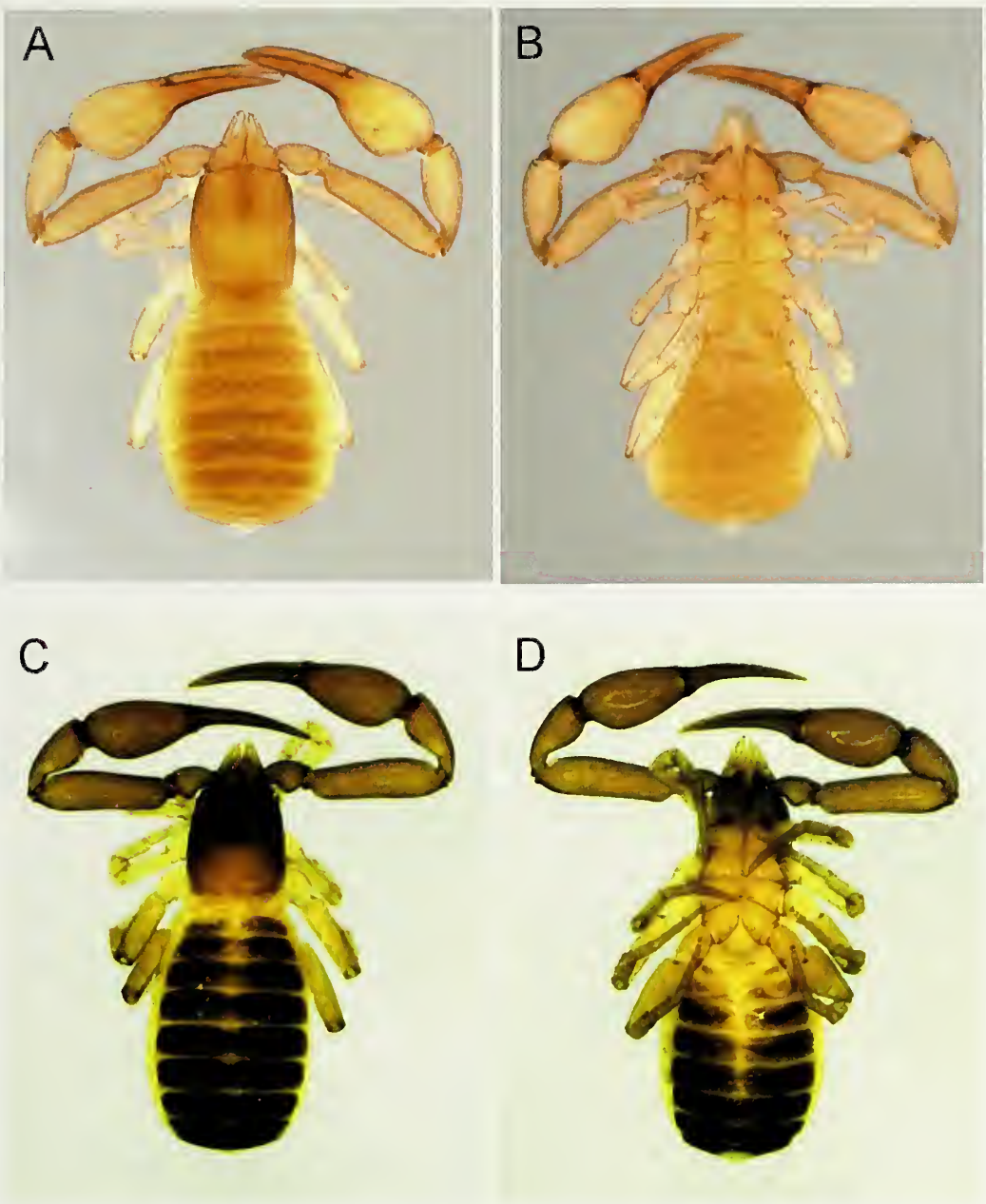

Figure 1.—A, B. *Albiorix parvidentatus* Chamberlin, female from Tucson, Arizona, USA. (WAM T129656); C, D. *Pseudalbiorix veracruzensis* (Hoff), male from Acatlán, Oaxaca, Mexico (WAM T65487): A, C, dorsal; B, D, ventral.

(e.g., Vachon 1964), there is a progressive addition of trichobothria at each post-embryonic stage. The general pattern of triehobothrial development in New World ideoroncids is similar between species, with a pattern of 3/1 in protonymphs, 9/6 in deutonymphs, 14–15/8 in tritonymphs and 20–22/10 in adults (Table 1). These figures exclude the occasional variation in total trichobothrial numbers when individual trichobothria are occasionally added or are lost (e.g., Mahnert 1984a; Table 1).

Ideoroncid protonymphs have three trichobothria on the fixed finger (*eb*, *et* and *ist*) and one on the movable finger (*t*), forming a pattern of 3/1, which is standard for all pseudoscorpions. The deutonymphal stage of Iocheirata is usually characterized by a 6/2 pattern, although reductions to slightly lower numbers oceur in species with reduced adult trichobothria (Harvey 1987, 2011; Mahnert 1984b; Vitali-di Castri 1965). The New World ideoroncid deutonymphs have extra trichobothria in the *ist* (for a total of 2) and *t* (4) regions, and the de novo addition of trichobothria in the *est* (2), *ib* (2), *it* (1) and *b* (2) regions. Tritonymphs have extra trichobothria in the *est* (4–5), *ib* (3–4), *ist* (3) and *t* (5) regions, and the *de novo* addition of trichobothria in the *esb* (1) and *st* (1) regions. The adults have additional trichobothria in the *est* (6), *ib* (4–6), *ist* (4–6) and *t* (6) regions, and the *de novo* addition of trichobothria in the *isb* (1) and *sb* (1) regions.

The slight differences observed in the tritonymphs of different species are not always reflected in the corresponding adults; i.e., those tritonymphs with a pattern of 14/8 have adults with a

Table 1.—The number of trichobothria occurring on New World species of Ideoroncidae, including known nymphal stages. Variant numbers are shown in parentheses.

		eb	*esb*	*est*	*et*	*ib*	*isb*	*ist*	*it*	*b*	*sb*	*st*	*t*	Fixed finger, total	Movable finger, total	Reference
Albiorix anophthalmus	Adult	1	1	6	1	5	1	6	1	2	1	1	6	22	10	This study
	Deutonymph	1	-	2	1	2	-	2	1	2	-	-	4	9	6	This study
Albiorix argentiniensis	Adult	1	1	6	1	4	1	5	1	2	1	1	6	20	10	Mahnert (1984a)
Albiorix chilensis	Adult	1	1	6	1	4	1	5	1	2	1	1	6	20	10	This study
	Tritonymph	1	1	4	1	3	-	3	1	2	-	1	5	14	8	This study
	Deutonymph	1	-	2	1	2	-	2	1	2	-	-	4	9	6	This study
	Protonymph	1	-	-	1	-	-	1	-	-	-	-	1	3	1	This study
Albiorix conodentatus	Adult	1	1	6	1	5	1	6	1	2	1	1	6	22	10	This study
	Tritonymph	1	1	5	1	3	-	3	1	2	-	1	5	15	8	This study
	Deutonymph	1	-	2	1	2	-	2	1	2	-	-	4	9	6	This study
Albiorix edentatus	Adult	1	1	6	1	4	1	6	1	2	1	1	6	21	10	This study
	Tritonymph	1	1	5	1	3	-	3	1	2	-	1	5	15	8	This study
Albiorix gertschi	Adult	1	1	6	1	5	1	6	1	2	1	1	6	22	10	This study
Albiorix magnus	Adult	1	1	6	1	5	1	6	1	2	1	1	6	22	10	This study
Albiorix meraculus	Adult	1	1	6	1	5	1	6	1	2	1	1	6	22	10	This study
	Tritonymph	1	1	4	1	3	-	3	1	2	-	1	5	14	8	This study
Albiorix mexicanus	Adult	1	1	6	1	4	1	5	1	2	1	1	6	20	10	Mahnert (1984a); this study
	Tritonymph	1	1	4	1	3	-	3	1	2	-	1	5	14	8	This study
Albiorix minor	Adult	1	1	6	1	5	1	6 (4, 5)	1	2	1	1	6	22 (20, 21)	10	This study
Albiorix mirabilis	Adult	1	1	6	1	5	1	6	1	2	1	1	6	22	10	This study
Albiorix oaxaca	Adult	1	1	6	1	5	1	6	1	2	1	1	6	22	10	This study
Albiorix parvidentatus	Adult	1	1	6	1	5 (4)	1	6 (4, 5)	1	2	1	1	6	22 (20, 21)	10	This study
	Tritonymph	1	1	5	1	3	-	3	1	2	-	1	5	15	8	This study
Albiorix puebla	Adult	1	1	6	1	5	1	6	1	2	1	1	6	22	10	This study
Albiorix retrodentatus	Adult	1	1	6	1	5	1	6	1	2	1	1	6	22	10	This study
	Tritonymph	1	1	5	1	3	-	3	1	2	-	1	5	15	8	This study
Albiorix rosario	Adult	1	1	6	1	5	1	6	1	2	1	1	6	22	10	This study
Albiorix sarahae	Adult	1	1	6	1	4	1	6	1	2	1	1	6	21	10	This study
Albiorix vigintus	Adult	1	1	6	1	5	1	4	1	2	1	1	6	20	10	This study
Ideoroncus anophthalmus	Adult	1	1	6	1	4	1	5	1	2	1	1	6	20	10	Mahnert (1984a)
Ideoroncus beieri	Adult	1	1	6	1	4	1	6 (5)	1	2	1	1	6	21 (20)	10	Mahnert (1984a)
Ideoroncus cavicola	Adult	1	1	6	1	4	1	5	1	2	1	1	6	20	10	(Mahnert 2001)
Ideoroncus divisus	Adult	1	1	6	1	4	1	4	1	2	1	1	6	21	10	Mahnert (1984a)
	Tritonymph	1	1	4	1	3	-	3	1	2	-	1	5	14	8	Mahnert (1984a)
Ideoroncus lenkoi	Adult	1	1	6	1	4	1	5	1	2	1	1	6	20	10	Mahnert (1984a)
	Tritonymph	1	1	4	1	3	-	3	1	2	-	1	5	14	8	Mahnert (1984a)
Ideoroncus pallidus	Adult	1	1	6	1	4	1	5	1	2	1	1	6	20	10	Mahnert (1984a)
Ideoroncus paranensis	Adult	1	1	6	1	4	1	5	1	2	1	1	6	20	10	Mahnert (1984a)
	Tritonymph	1	1	4	1	3	-	3	1	2	-	1	5	14	8	Mahnert (1984a)
Ideoroncus procerus	Adult	1	1	6	1	4 (5)	1	6	1	2	1	1	6	21 (22)	10	Mahnert (1984a)
Ideoroncus setosus	Adult	1	1	6	1	4	1	5	1	2	1	1	6	20	10	Mahnert (1984a)
	Tritonymph	1	1	4	1	3	-	3	1	2	-	1	5	14	8	Mahnert (1984a)
	Deutonymph	1	-	2	1	2	-	2	1	2	-	-	4	9	6	Mahnert (1984a)
	Protonymph	1	-	-	1	-	-	1	-	-	-	-	1	3	1	Mahnert (1984a)
Mahnertius hadrodentatus	Adult	1	1	6	1	5	1	6	1	2	1	1	6	22	10	This study
Mahnertius stipodentatus	Adult	1	1	6	1	5	1	6	1	2	1	1	6	22	10	This study
Muchmoreus ignotus	Adult	1	1	6	1	4	1	5	1	2	1	1	6	20	10	This study
	Tritonymph	1	1	4	1	3	-	3	1	2	-	1	5	14	8	This study
Pseudalbiorix armasi	Adult	1	1	6	1	4	1	5	1	2	1	1	6	20	10	Harvey et al. (2007)
	Tritonymph	1	1	4	1	3	-	3	1	2	-	1	5	14	8	Harvey et al. (2007)
Pseudalbiorix muchmorei	Adult	1	1	6	1	4	1	5	1	2	1	1	6	20	10	Harvey et al. (2007)
Pseudalbiorix reddelli	Adult	1	1	6	1	4	1	5	1	2	1	1	6	20	10	Harvey et al. (2007)
	Tritonymph	1	1	4	1	3	-	3	1	2	-	1	5	14	8	Harvey et al. (2007)
	Deutonymph	1	-	2	1	2	-	2	1	2	-	-	4	9	6	Harvey et al. (2007)
	Protonymph	1	-	-	1	-	-	1	-	-	-	-	1	3	1	Harvey et al. (2007)
Pseudalbiorix veracruzensis	Adult	1	1	6	1	4	1	5	1	2	1	1	6	20	10	Harvey et al. (2007)
	Tritonymph	1	1	4	1	3	-	4	1	2	-	1	5	15	8	Harvey et al. (2007)
Typhloroncus attenuatus	Adult	1	1	6	1	4	1	7	1	2	1	1	6	22	10	This study

Table 1.—Continued.

		eb	*esb*	*est*	*et*	*ib*	*isb*	*ist*	*it*	*b*	*sb*	*st*	*t*	Fixed finger, total	Movable finger, total	Reference
Typhloroncus coralensis	Adult	1	1	6	1	4	1	7	1	2	1	1	6	22	10	This study
Typhloroncus diabolus	Adult	1	1	6	1	4	1	7	1	2	1	1	6	22	10 (11)	This study
Typhloroncus planodentatus	Adult	1	1	6	1	5	1	6	1	2	1	1	6	22	10	This study
Typhloroncus troglobius	Adult	1	1	6	1	4	1	7	1	2	1	1	6	22	10	This study
Typhloroncus xilitlensis	Adult	1	1	6	1	4	1	7	1	2	1	1	6	22	10	Muchmore (1986)
Xorilbia arboricola	Adult	1	1	6	1	5	1	6	1	2	1	1	6	22	10	Mahnert (1984a)
	Tritonymph	1	1	4	1	4	-	3	1	2	-	1	5	15	8	Mahnert (1984a)
	Protonymph	1	-	-	1	-	-	1	-	-	-	-	1	3	1	Mahnert (1979)
Xorilbia gracilis	Adult	1	1	6	1	5	1	6	1	2	1	1	6	22	10	Mahnert (1985b)
	Tritonymph	1	1	4	1	4	-	3	1	2	-	1	5	15	8	Mahnert (1985b)
	Protonymph	1	-	-	1	-	-	1	-	-	-	-	1	3	1	Mahnert (1985b)
Xorilbia lamellifer	Adult	1	1	6	1	5	1	6	1	2	1	1	6	22	10	Mahnert (1985b)

pattern of 20/10 (*A. chilensis*, *A. mexicanus*, *Ideoroncus lenkoi*, *I. paranensis*, *I. setosus*, *M. iguotus*, *P. armasi*, *P. reddelli*), 21/10 (*I. divisus*) or 22/10 (*A. meraculus*), and those tritonymphs with a pattern of 15/8 have adults with 20/10 (*P. veracruzensis*), 21/10 (*A. edentatus*) or 22/10 (*A. conodentatus*, *A. parvidentatus*, *A. retrodentatus*, *Xorilbia arboricola* and *X. gracilis*).

Other significant differences between the various life stages include the lack of a cheliceral galeal seta and the absence of a posterior maxillary lyrifissure in all protonymphs.

Subterminal tarsal seta.—The paired subterminal tarsal setae achieve several different morphologies in the Ideoroncidae. They are bifurcate or trifurcate in most species, but are completely acuminate in *Typhloroncus planodentatus*, *T. xilitlensis* and species of *Xorilbia*. The greatest intra-generic variation was found in *Albiorix*, where it ranged from trifurcate with all tines short and sub-equal in length (e.g., Figs. 10G, 15D), to trifurcate with long tines (Fig. 13E), to trifurcate with one tine much longer than the others (Fig. 18E) to bifurcate with long tines (Figs. 14F, 22E). The morphology was found to be consistent on all legs of an individual, and was constant between species and each post-embryonic stage.

Distribution.—The family Ideoroncidae occurs in east Africa, Asia, and the Americas. Although mostly confined to tropical biotypes, they also inhabit temperate habitats in North and South America (Fig. 2). They have been mostly found in leaf litter or on the underside of rocks, but some species live within caves where they have developed into highly modified troglobites with long appendages and no eyes (Muchmore 1982b; Muchmore & Pape 1999).

The New World fauna is patchily distributed and most genera are allopatric, with the only zone of overlap being southern Mexico where species of *Albiorix* coincide with species of *Typhloroncus* and *Pseudalbiorix* (Fig. 2). *Albiorix* occurs in southwestern USA and Mexico, as well as two outlying species in Chile and Argentina (Fig. 2A). The remaining South American fauna consists of *Xorilbia* in the Amazon region, *Mahnertius* in Colombia, and *Ideoroncus* in southern Brazil and neighboring Paraguay (Fig. 2). The remaining American ideoroncid genera are *Muchmoreus*, which is restricted to the Yucatan Peninsula, *Pseudalbiorix* in southern Mexico and adjacent countries, and *Typhloroncus* with species from Mexico and the US Virgin Islands (Fig. 2).

Remarks.—Ideoroncidae is an easily recognized family, which was suggested to be the sister-group to the family Bochicidae by Harvey (1992). This result was not confirmed by Harvey & Volschenk (2007) in an analysis of several exemplar species of the seven families of Neobisioidea. Instead, they found that Ideoroncidae was sister to all other Neobisioidea, with the exception of the Bochicinae. Both results suggest that the Ideoroncidae are a relatively basal clade of Neobisioidea.

KEY TO NEW WORLD GENERA OF IDEORONCIDAE

1. Arolium much longer than claws and without ventral hooked process (e.g., Figs. 8A, 29I) 2
   Arolium shorter than claws or same length as claws and with ventral hooked process (e.g., Figs. 27F, 31D) 5
2. Arolium deeply divided (e.g., Figs. 9D, 21G) ..... *Albiorix*
   Arolium not divided (Fig. 29I) 3
3. Condyle on external margin of chelal hand large and bifurcate ..... *Pseudalbiorix*
   Chelal hand with retrolateral condyle small and rounded 4
4. Sternites with median suture line; each spiracular plate with 1 seta ..... *Ideoroncus*
   Sternites without median suture line; each spiracular plate with 2 or 3 setae ..... *Muchmoreus*
5. Distal teeth of fixed chelal finger raised into a short ridge (Fig. 28H) ..... *Mahnertius*
   Distal teeth of fixed chelal finger not raised into a short ridge (Fig. 31E) 6
6. Arolium divided; anal operculum not abutting sternite X ..... *Xorilbia*
   Arolium not divided; anal operculum either closely abutting or adjacent to sternite X (Figs. 30A–C) ..... *Typhloroncus*

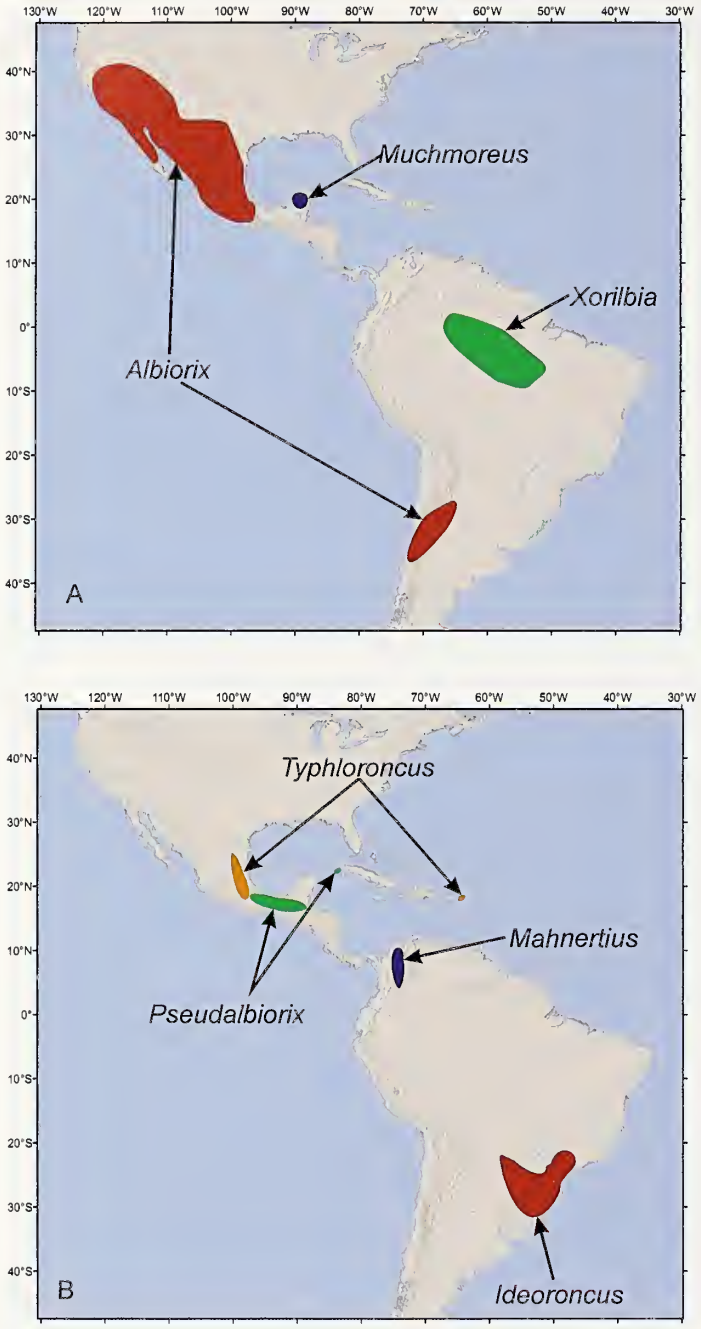

Figure 2.—Distribution of the genera of Ideoroncidae in the New World: A. *Albiorix*, *Muchmoreus* and *Xorilbia*; B. *Ideoroncus*, *Mahnertius*, *Pseudalbiorix* and *Typhloroncus*.

Albiorix Chamberlin 1930

Albiorix Chamberlin 1930:44; Beier 1932a:172; Hoff 1945:1; Hoff 1956:25; Mahnert 1984a:671; Harvey 1991:316; Harvey 2013:unpaginated.

Dinoroncus Beier 1931:305; Beier 1932a:171 (synonymized by Mahnert 1984a:676).

Type species.—*Albiorix: Ideoroncus mexicanus* Banks 1898, by original designation *Dinoroncus*: *Ideobisium (Ideoroncus) chilense* Ellingsen 1905, by original designation.

Diagnosis.—Species of *Albiorix* possess deeply divided arolia (e.g., Figs. 9D, 21G), a feature that is nearly unique within the Ideoroncidae, and that elsewhere amongst pseudoscorpions is restricted to most species of Garypinidae. Species of *Xorilbia* also have divided arolia, but unlike *Albiorix*, the arolia are shorter than the elaws and the arolium has a ventral hook.

Description.—*Adult:* setae: long, straight and acicular.

Chelicera (Figs. 7A, 7B): hand usually with 6 setae, occasionally with 5 or very rarely 7 setae; movable finger with 1 long subdistal seta; rallum of 4 thickened blades (Fig. 7C), all blades serrate in some species, only the two distal blades serrate in others; lamina exterior absent; galea long and slender.

Pedipalp: long and slender; patella with disto-prolateral excavation; fixed chelal finger and hand with 20 or 22 trichobothria (very rarely 19 or 21), movable chelal finger with 10 trichobothria (e.g., Fig. 4): *eb* region with 1 trichobothrium; *est* region with 6 (5 in one specimen) trichobothria; *ib* region with 4 or 5 trichobothria; *ist* region with 5 or 6 trichobothria; *b* region with 2 trichobothria; *sb* and *st* regions with 1 trichobothrium; and *t* region with 6 trichobothria; *st* not ventrally displaced. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus near *est* region in fixed finger and near *t* region in movable finger; chelal teeth all closely spaced; base of fixed chelal finger with several small denticles (Figs. 7D, 7E); chelal hand with retrolateral condyle small and rounded (Fig. 7E).

Carapace: with 2 small, bulging eyes (e.g., Figs. 10A, 15E), or absent (Fig. 8A); without furrows or with faint posterior furrow near posterior margin; anterior margin with 4 or occasionally 6 setae.

Coxal region (Fig. 6A): manducatory process with 2 long distal setae; median maxillary lyrifissure present and subbasally situated.

Legs (Figs. 7F, 7G): femora I and II without basal swelling; femora I and II with primary slit sensillum directed transversely; femur I much longer than patella I; suture line between femur IV and patella IV transverse; metatarsus shorter than tarsus; metatarsal pseudotaetile seta sub-proximal; legs with subterminal tarsal setae either bifurcate or trifurcate; arolium longer than claws, deeply divided (e.g., Figs. 9D, 21G), without ventral hooked protuberance; without sub-ungual spine; claws slender and simple.

Abdomen: tergites and sternites undivided. Pleural membrane longitudinally striate (Fig. 6F). Each stigmatic sclerite with 1 seta (Fig. 6E); spiracles simple, with spiracular helix. Anterior margin of anal operculum not abutting posterior margin of sternite X (Fig. 7H).

Genitalia: male median genital sac bipartite (Fig. 6B); female with large gonosac covered with scattered pores (Fig. 6C); setae of anterior genital operculum (sternite II) of female very small (Fig. 6D).

Tritonymph: Pedipalp: fixed finger with 14 or 15 trichobothria, movable finger with 8 trichobothria (e.g., Figs. 4C, 10E, 11E, 14E, 15B, 16E); *eb*, *esb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 3 trichobothria; *ist* region with 3 trichobothria; *est* region with 4 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *st* region with 1 trichobothrium; *t* region with 5 trichobothria; *isb* and *sb* absent.

Deutonymph: Pedipalp: fixed finger with 9 trichobothria, movable finger with 6 trichobothria (e.g., Figs. 4B, 10H, 11F);

eb, *ist*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 2 trichobothria; *est* region with 3 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *t* region with 4 trichobothria; *esb*, *isb*, *sb* and *st* absent.

Protonymph: Pedipalp: *eb*, *et*, *ist* and *t* regions each with 1 trichobothrium; others absent (Fig. 4A).

Remarks.—The genus *Albiorix* was erected by Chamberlin (1930) for three species of ideoroncid pseudoscorpions from Mexico and southwestern USA each possessing long, divided arolia. The type species, *Ideoroncus mexicanus* Banks, was recorded by Chamberlin (1930) as *A. mexicanus* throughout the western USA and Mexico, whereas *A. parvidentatus* Chamberlin and *A. edentatus* Chamberlin were restricted to California. Several species have been subsequently added to the genus from the New World (Hoff 1945, 1950; Beier 1963; Muchmore 1982b; Muchmore & Pape 1999), but some have since been removed to other genera. *Albiorix reddelli* Muchmore 1982 and *A. veracruzensis* Hoff 1945 were transferred to the new genus *Pseudalbiorix* by Harvey et al. (2007), as they lack the long, divided arolia characteristic of *Albiorix*, and have a bifid retrolateral chelal condyle that is lacking in *Albiorix*. Although *A. arboricola* Mahnert 1979, *A. gracilis* Mahnert 1985 and *A. lanellifer* Mahnert 1985 from Amazonian Brazil have divided arolia (Mahnert 1984a, 1985b), the arolium of these species is distinctly shorter than the claws and possesses a small ventral hook (Harvey & Mahnert 2006, Fig. 1; Mahnert 1984a, Fig. 41). This hook is absent in the remaining species of *Albiorix*, but occurs in other ideoroncids including *Dhanus siamensis* (With 1906) and in species of *Negroroncus* and *Typhloroncus* (Vachon 1958; M.S. Harvey pers. obs.). These differences led Harvey & Mahnert (2006) to transfer the three Brazilian *Albiorix* species to the new genus *Xorilbia*.

The genus *Dinoroncus* was established by Beier (1931) for *Ideobisium (Ideoroncus) chilense* Ellingsen 1905, which was described from a single specimen from Santiago, Chile (Ellingsen 1905). New records of this species were reported by Feio (1945) from La Rioja Province in northwestern Argentina, and Hoff (1950) added a second species to the genus, *D. argentiniensis* Hoff 1950, from La Sébila, also in La Rioja Province, Argentina. Hoff (1950) also suggested that the Argentinian records of *D. chilensis* were most likely misidentified specimens of *D. argentiniensis*. Although Mahnert (1984a) was unable to examine any specimens of *I. chilense*, his study of *D. argentiniensis* led him to believe that the genus *Dinoroncus* should be regarded as a synonym of the genus *Albiorix*, as the latter species possessed the deeply divided arolium characteristic of that genus. Our study of the holotype of *I. chilense* and other specimens attributed to that species has revealed that they indeed have long, divided arolia (Fig. 9D), and the synonymy of *Dinoroncus* with *Albiorix* is confirmed.

Etymology.—Chamberlin (1930) did not provide an etymology for the genus *Albiorix*, but Harvey et al. (2007) assumed it was named for the Celtic god Albiorix. Chamberlin (1930) also did not specifically nominate a gender for *Albiorix*, but the three species originally included were treated as masculine (*A. mexicanus*, *A. edentatus* and *A. parvidentatus*), and subsequent authors have since added obviously masculine names (Hoff 1945; Muchmore & Pape 1999), confirming that the genus name is masculine.

KEY TO SPECIES OF *ALBIORIX*

1. One pair of eyes present (e.g., Figs. 17A, 23A) 2
   Eyes completely absent (Fig. 8A) ..... *A. anophthalmus*
2. Chelicera with 5 setae (Fig. 7B); anterior margin of carapace with 6 setae (Fig. 9B); trichobothrium *ib* region of chelal hand with 4 trichobothria (Figs. 5B, 9E); trichobothrium *t* region overlapping with *est* region (Figs. 5B, 9E) ..... *A. chilensis*
   Chelicera with 6 setae (Fig. 7A); anterior margin of carapace with 4 setae (Figs. 13A, 18A); trichobothrium *ib* region of chelal hand with 5 trichobothria (Figs. 5F, 5G, 5K); trichobothrium *t* region distal to *est* region (Figs. 5F, 5G, 5K, 13C, 14C, 15C) 3
3. Chelal hand completely smooth (Fig. 17B) ..... *A. mirabilis*
   Chelal hand with prolateral and, usually, retrolateral margins granulate, sometimes weakly so (e.g., Figs. 13B, 19B, 23B) .. 4
4. Subterminal tarsal seta bifurcate (Figs. 14F, 22E) 5
   Subterminal tarsal seta trifurcate (e.g., Figs. 13E, 19F, 21G) 6
5. Subterminal tarsal seta with each tine very long (Fig. 14F) ..... *A. meraculus*
   Subterminal tarsal setae with each tine short (Fig. 22E) ..... *A. rosario*
6. Subterminal tarsal seta with 1 very long distal tine and 2 short basal tines (Fig. 18E) ..... *A. oaxaca*
   Subterminal tarsal seta with each tine short and of similar length (e.g., Figs. 13E, 19F, 21G) 7
7. Larger species, e.g., chela (with pedicel) greater than 1.9 mm in length ..... *A. magnus*
   Smaller species, e.g., chela (with pedicel) less than 1.9 mm in length 8
8. Chelal teeth of the fixed finger very closely spaced (Figs. 13C, 13D); trichobothrium est_4 situated basally, overlapping with *ist* group (Figs. 5C, 9C) ..... *A. conodentatus*
   Chelal teeth of the fixed finger not so closely spaced (e.g., Figs. 11D, 19D, 21D); trichobothrium est_4 situated distally, never overlapping with *ist* group (e.g., Figs. 19C, 21C, 23C) 9
9. Teeth of fixed chelal finger very low, much longer than high (Fig. 11D) ..... *A. edentatus*
   Teeth of fixed chelal finger higher than long (e.g., Figs. 15C, 21D) 10
10. Tips of the teeth of the fixed chelal finger sharply pointed (Fig. 15C) ..... *A. mexicanus*
    Tips of the teeth of the fixed chelal finger slightly rounded (e.g., Figs. 12D, 21D) 11
11. Median teeth of fixed chelal finger with noticeably sinuate distal face (Figs. 20D, 21D) 12
    Median teeth of fixed chelal finger with straight or slightly sinuate distal face (e.g., Figs. 16D, 19D) 13
12. Larger species, e.g. chela (with pedicel) greater than 1.2 (male) mm in length; trichobothrium ist_1 slightly dorso-distal to ist_3 (Fig. 21C) ..... *A. retrodentatus*

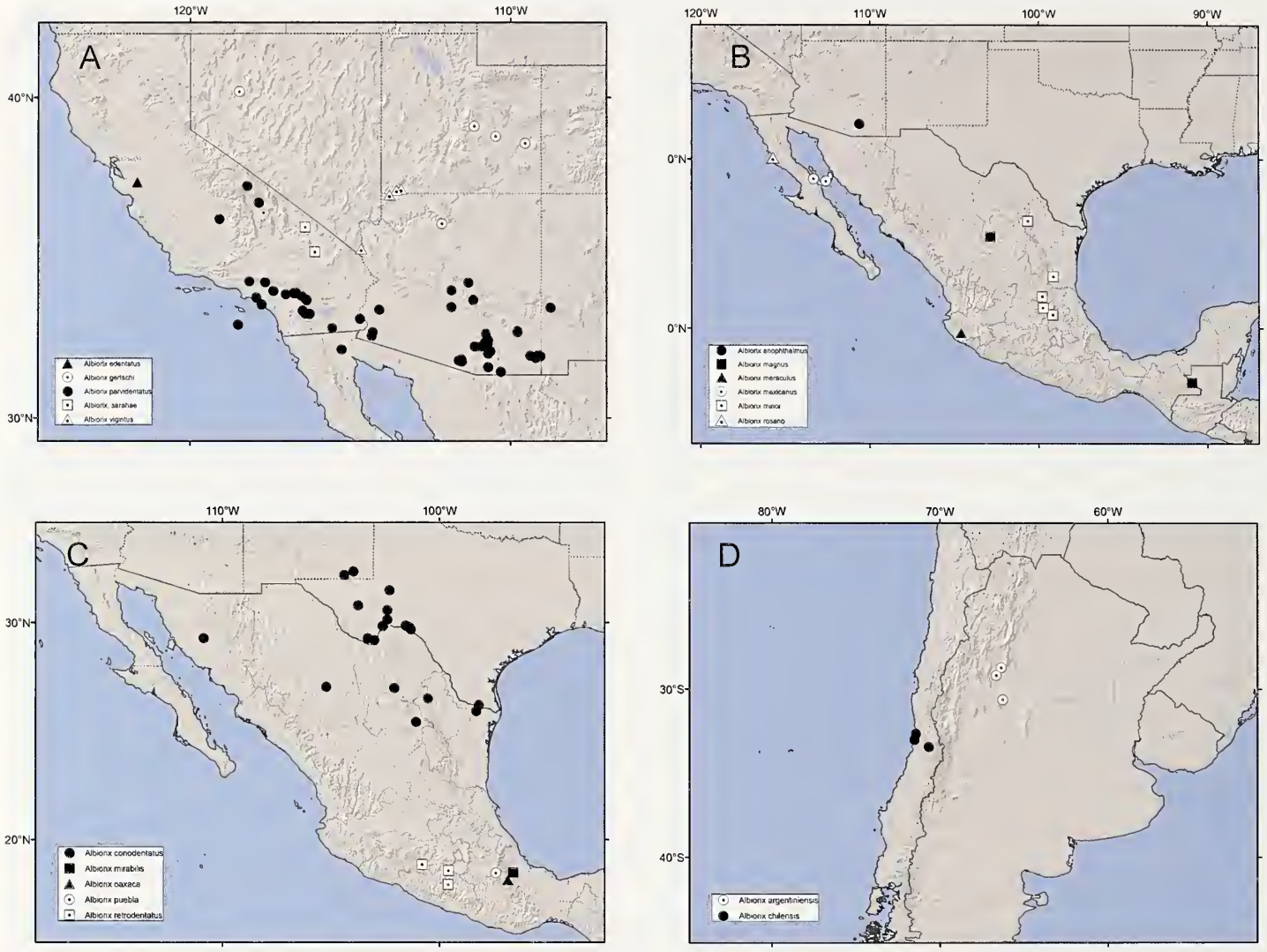

Figure 3.—Distribution of *Albiorix* species.

Smaller species, e.g., chela (with pedicel) less than 1.0 (male) mm in length; trichobothrium ist_1 directly dorsal to ist_3 (Fig. 20C) . . . . . *A. puebla*

13. Trichobothrium ib_5 distally displaced, situated far distal of *eb*, *esb* and *isb* (Figs. 12C, 23C, 24B) 14
    Trichobothrium ib_5 not distally displaced, situated about on same level as *eb*, *esb* and *isb* (Figs. 16C, 19C) 16
14. Fixed chelal finger and hand with 22 trichobothria, with ist_1 present (Figs. 12B, 12C) . . . . . *A. gertschi*
    Fixed chelal finger and hand with 20 or 21 trichobothria, with ist_1 absent (Figs. 23B, 23C, 24A, 24B) 15
15. Fixed chelal finger and hand with 20 trichobothria, *ist* region with 4 trichobothria (Fig. 24B) . . . . . *A. vigintus*
    Fixed chelal finger and hand with 21 trichobothria, *ist* region with 5 trichobothria (Fig. 23C) . . . . . *A. sarahae*
16. Larger species, e.g., chela (without pedicel) 1.67 (female) mm in length . . . . . *A. argentiniensis*
    Smaller species, e.g. chela (without pedicel) less than 1.5 (female) mm in length 17
17. Teeth of fixed chelal finger only slightly longer than high (Fig. 16D) . . . . . *A. minor*
    Teeth of fixed chelal finger noticeably longer than high (Fig. 19D) . . . . . *A. parvidentatus*

Albiorix anophthalmus Muchmore 1999
Figs. 3B, 5A, 8

Albiorix anophthalmus Muchmore, in Muchmore and Pape 1999:138–141, Figs. 1a–c, 2, 4; Harvey 2013:unpaginated.

Types examined.—USA: *Arizona*: Holotype male, Arkenstone Cave, Colossal Cave Mountain Park, Pima County (32°04′N, 110°38′W), 9 September 1990, R.B. Pape (FSCA, WM7541.01001). Paratypes: USA: *Arizona*: 1 female (allotype), same data as holotype, except 22 March 1992 (FSCA, WM7807.01001); 1 male, same data as holotype, except 11 August 1990 (FSCA, WM7540.01001); 1 deutonymph, same data as holotype, except 9 June 1991 (FSCA, WM7707.01001).

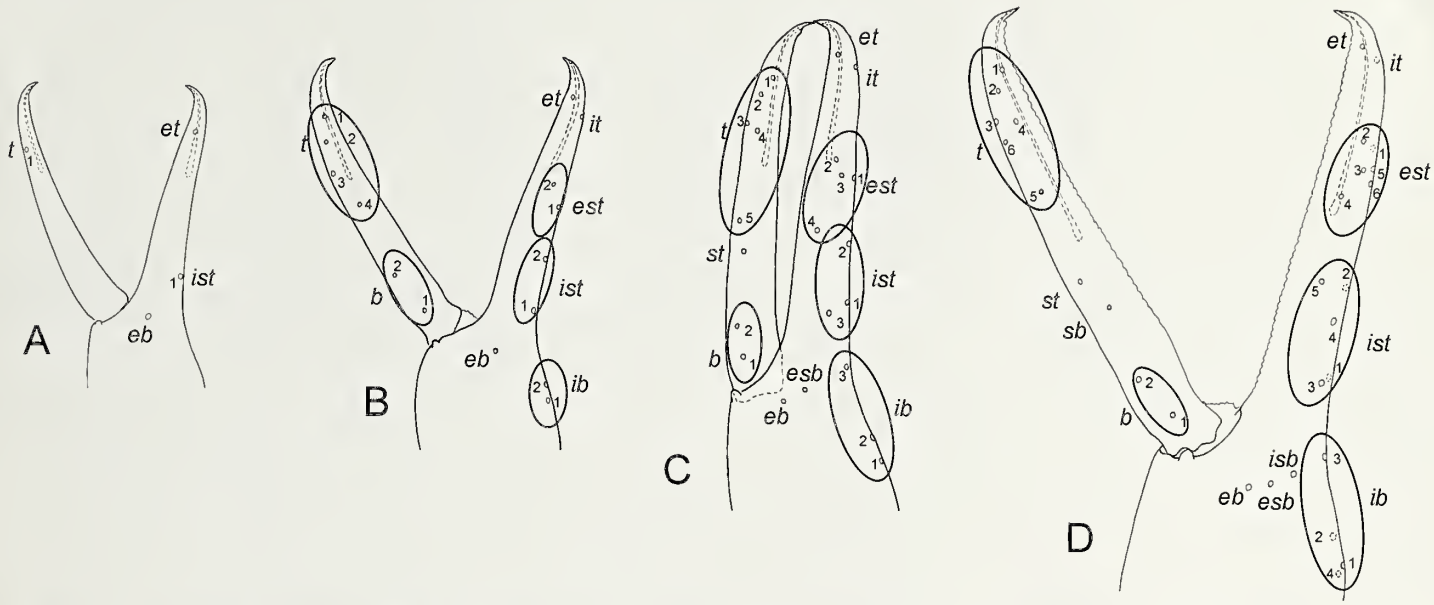

Figure 4.—Left chela (or a mirror image of the right chela), post-embryonic trichobothrial patterns of *Albiorix chilensis* (Ellingsen), specimens from 1 km E. of Maitencillo (UCDC), unless stated otherwise: A. Protonymph; B. Deutonymph; C. Tritonymph (UCDC, Jardin Botanico Nacional); D. Adult male.

Other material examined.—USA: *Arizona*: 1 female, Colossal Cave, Pima County (32°04′N, 110°38′W), no date, J. Cowles (WAM T91621).

Diagnosis.—This highly troglomorphic species is the only known species of *Albiorix* that lacks eyes (Fig. 8A).

Description.—*Adult:* See Muchmore & Pape (1999), except as follows: Pedipalp: fixed chelal finger and hand with 22 trichobothria, movable chelal finger with 10 trichobothria (Figs. 5A, 8C): *eb*, *esb* and *isb* in straight row at base of finger; *eb*, *esb*, *isb*, *it* and *et* regions each with 1 triehobothrium; *ib* region with 5 trichobothria; *ist* region with 6 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region; base of fixed chelal finger with several small denticles.

Deutonymph: Chelicera: galea long, slightly curved; hand with 5 setae, movable finger with 1 seta; rallum composed of 4 blades, all serrate.

Pedipalp: trochanter 2.15, femur 5.29, patella 3.57, chela (with pedicel) 4.97, chela (without pedicel) 4.73 × longer than broad. Fixed finger with 9 trichobothria, movable finger with 6 trichobothria (Fig. 8E); *eb*, *ist*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 2 trichobothria; *est* region with 3 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *t* region with 4 triehobothria; *esb*, *isb*, *sb* and *st* absent. Chelal hand with retrolateral condyle small and rounded.

Carapace: anterior margin medially prominent; eyes absent; with 4 setae on anterior margin and 2 setae on posterior margin.

Coxal region: posterior maxillary lyrifissure present, subbasal.

Legs: much as in adult.

Dimensions (mm): Body length ca. 1.87. Pedipalp: trochanter 0.237/0.110, femur 0.608/0.115, patella 0.446/0.125, chela (with pedicel) 1.004/0.202, chela (without pedicel) 0.955, hand (without pedicel) length 0.352, movable finger length 0.590. Carapace 0.557/? (distorted).

Remarks.—*Albiorix anophthalmus* is a highly modified blind troglobite known only from caves within the Colossal Cave Mountain Park in southern Arizona (Fig. 3B). Muchmore & Pape (1999) summarized numerous records within Arkenstone Cave where individuals were found on the underside of broken calcite pieces and limestone rocks on the floor of the cave.

We have reexamined the four type specimens collected in Arkenstone Cave used to compile the original description (Muchmore & Pape 1999), as well as an additional female collected in nearby Colossal Cave. Although the original description tentatively identified 20 trichobothria on the fixed chelal finger and hand (Muchmore & Pape 1999), we can now detect 22 trichobothria (Figs. 5A, 8C).

Albiorix argentinensis (Hoff 1950)
Fig. 3D

Dinoroncus chilensis (Ellingsen): Feio 1945:4 (misidentification).
Dinoroncus argentinensis Hoff 1950:229–232, Figs. 7–9.
Albiorix argentinensis (Hoff): Mahnert 1984a:675–676, Fig. 44; Harvey 1991:316; Ceballos & Ferradas 2008:109–110; Mahnert et al. 2011:9–10; Harvey 2013:unpaginated.

Material examined.—None. The holotype was originally lodged in the J.A. Rosas Costas collection, but subsequently destroyed by Rosas Costas himself (Mahnert et al. 2011).

Diagnosis.—*Albiorix argentinensis* is a moderately large species [e.g. chela (without pedicel 1.67 (female) mm in length]. It differs from *A. chilensis*, the only other South American species of *Albiorix*, by the trichobothrium *t* region not overlapping with the *est* region.

Description.—See Hoff (1950) and Mahnert (1984a).

Remarks.—We have not examined any specimens of this species, which has only been recorded from La Rioja Province in northwestern Argentina, including the type locality La Sébila (Hoff 1950), Bazán (incorrectly spelled 'Balzan' by

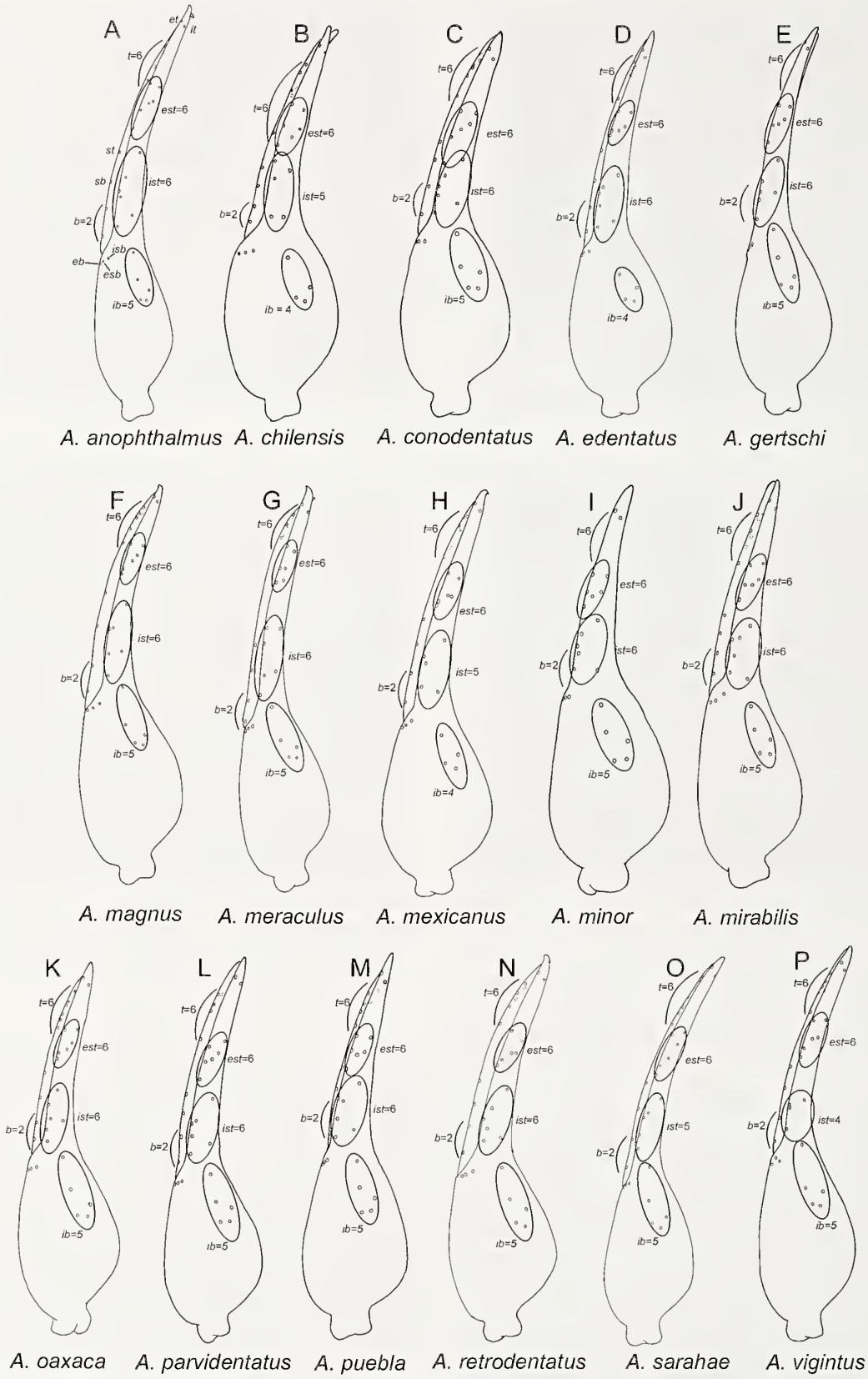

Figure 5.—Trichobothrial patterns of *Albiorix* species, taken from left chela (or a mirror image of the right chela). Not shown are *A. argentiniensis* (Hoff) (not studied) and *A. rosario* Harvey & Muchmore sp. nov. (sole specimen has the chela mounted laterally).

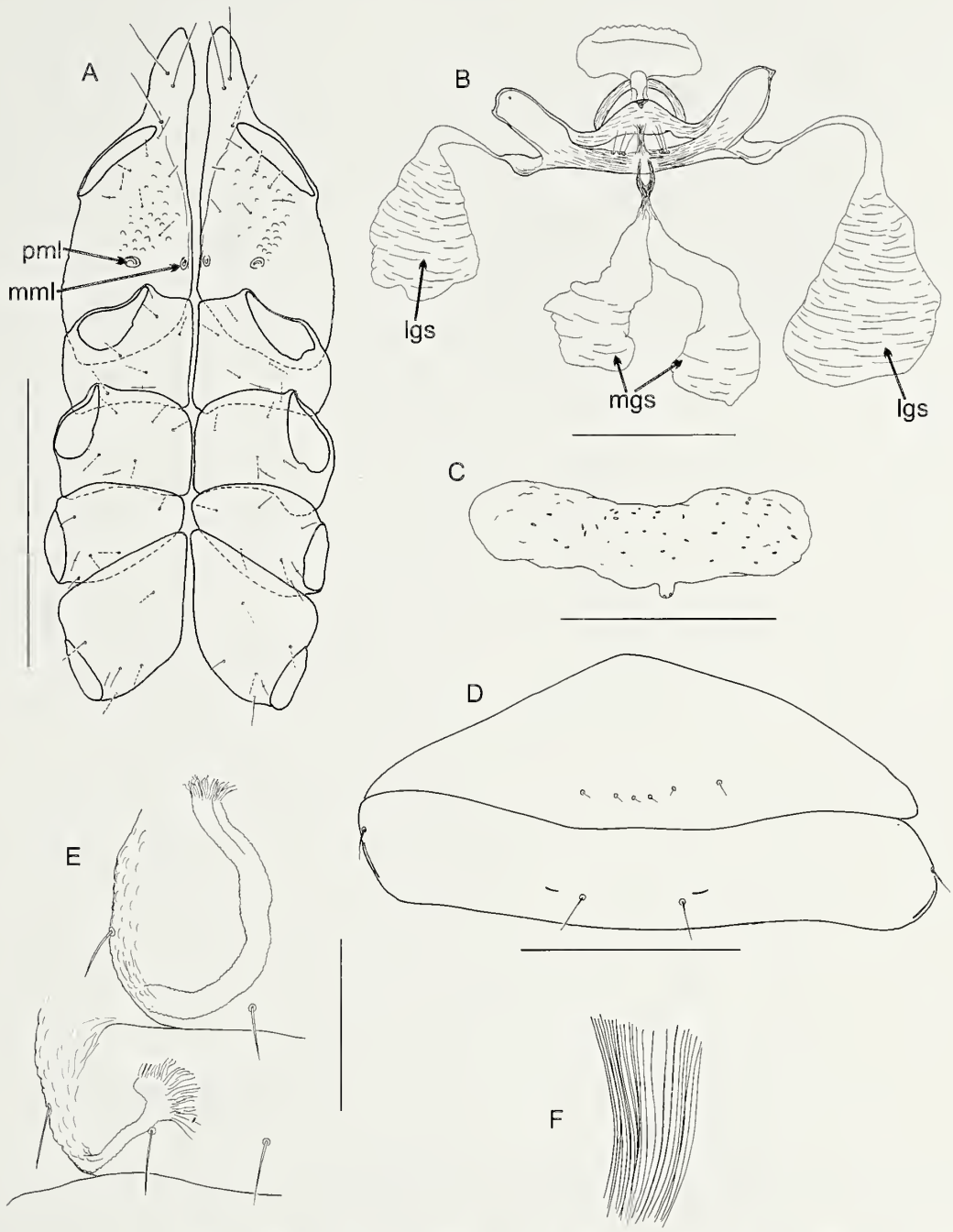

Figure 6.—*Albiorix* spp.: A. Coxal region, ventral [*A. mexicanus* (Banks), female neotype]; B. Male genitalia, ventral (*A. parvidentatus* Chamberlin, CAS, JC–1371.01001, male); C. Gonosac (*A. parvidentatus*, CAS, JC–375.02001, female); D. Sternites II and III (*A. parvidentatus*, CAS, JC–375.02001, female); E. Spiracular region, ventral (*A. parvidentatus*, CAS, JC–1371.01001, male); F. Pleural membrane (*A. parvidentatus*, CAS, JC–1371.01001, male). Abbreviations: lgs, lateral genital sac; mgs, median genital sac; mml, median maxillary lyrifissure; pml, posterior maxillary lyrifissure. Scale lines = 0.5 mm (A); 0.2 mm (C, D); 0.1 mm (B, E, F).

Feio) and Olta (Feio 1945) (Fig. 3D). The long and deeply divided arolium (Mahnert 1984a) confirms that this species is correctly placed in *Albiorix*.

Albiorix chilensis (Ellingsen 1905)
Figs. 3D, 4, 5B, 7B, 9

Ideobisium (Ideoroncus) chilense Ellingsen 1905:326–327.
Dinoroncus chilensis (Ellingsen): Beier 1931:305 [as *Dinoroncus chilense* [sic)]; Beier 1932a:172, Fig. 202; Roewer 1937:257; Beier 1964:324–325; Cekalovic 1984:13.
Albiorix chilensis (Ellingsen): Mahnert 1984a:676; Harvey 1991:316–317; Harvey 2013:unpaginated.
Not *Dinoroncus chilensis* (Ellingsen): Feio 1945:4 (misidentification; see *Albiorix argentiniensis* (Hoff)).

Material examined.—*Holotype*. CHILE: *Región Metropolitana*: female, Santiago (33°27′S, 70°40′W), 10 April 1899, F. Silvestri (MZUN).

Other material. CHILE: *Valparaíso*: 1 male, 1 female, 1 deutonymph, 1 protonymph, 1 km E. of Maitencillo ("Marteneillo" on labels) (32°39′S, 71°26′W), 16 March

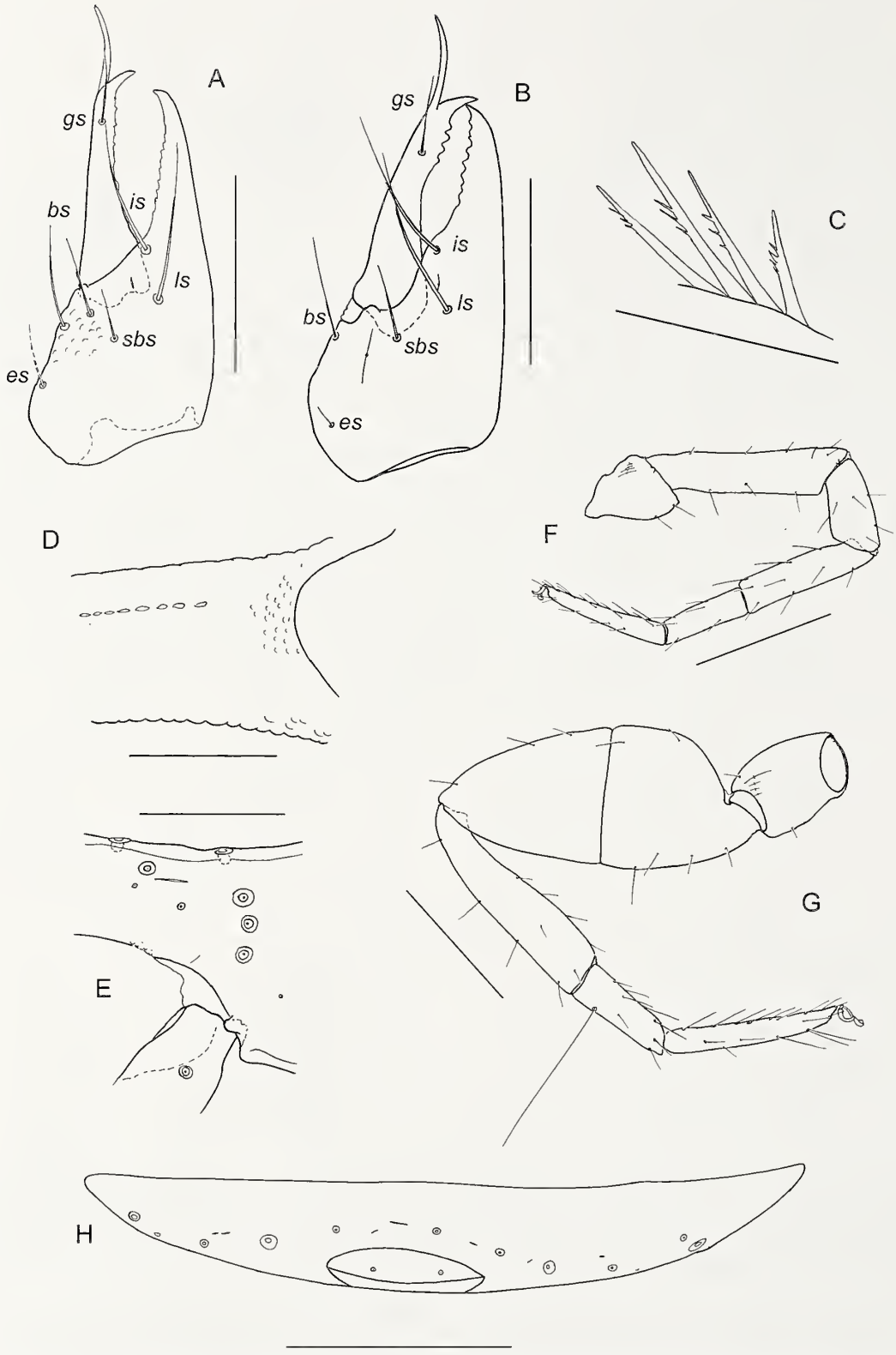

Figure 7.—*Albiorix* spp.: A. Left chelicera, dorsal [*A. mexicanus* (Banks), female neotype]; B. Left chelicera, dorsal [*A. chilensis* (Ellingsen), male]; C. Rallum (*A. mexicanus*, female neotype); D. Fixed chelal finger, showing denticles, ventral (*A. mexicanus*, female neotype); E. Chelal fingers, showing denticles, lateral (*A. parvidentatus*, male holotype); F. Left leg I (*A. parvidentatus*, male holotype); G. Right leg IV (*A. parvidentatus*, male holotype); H. Sternite XI (*A. parvidentatus*, CAS, JC–375.02001, female). Scale lines = 0.25 mm (B); 0.2 mm (A, F, G, H); 0.1 mm (C, D, E).

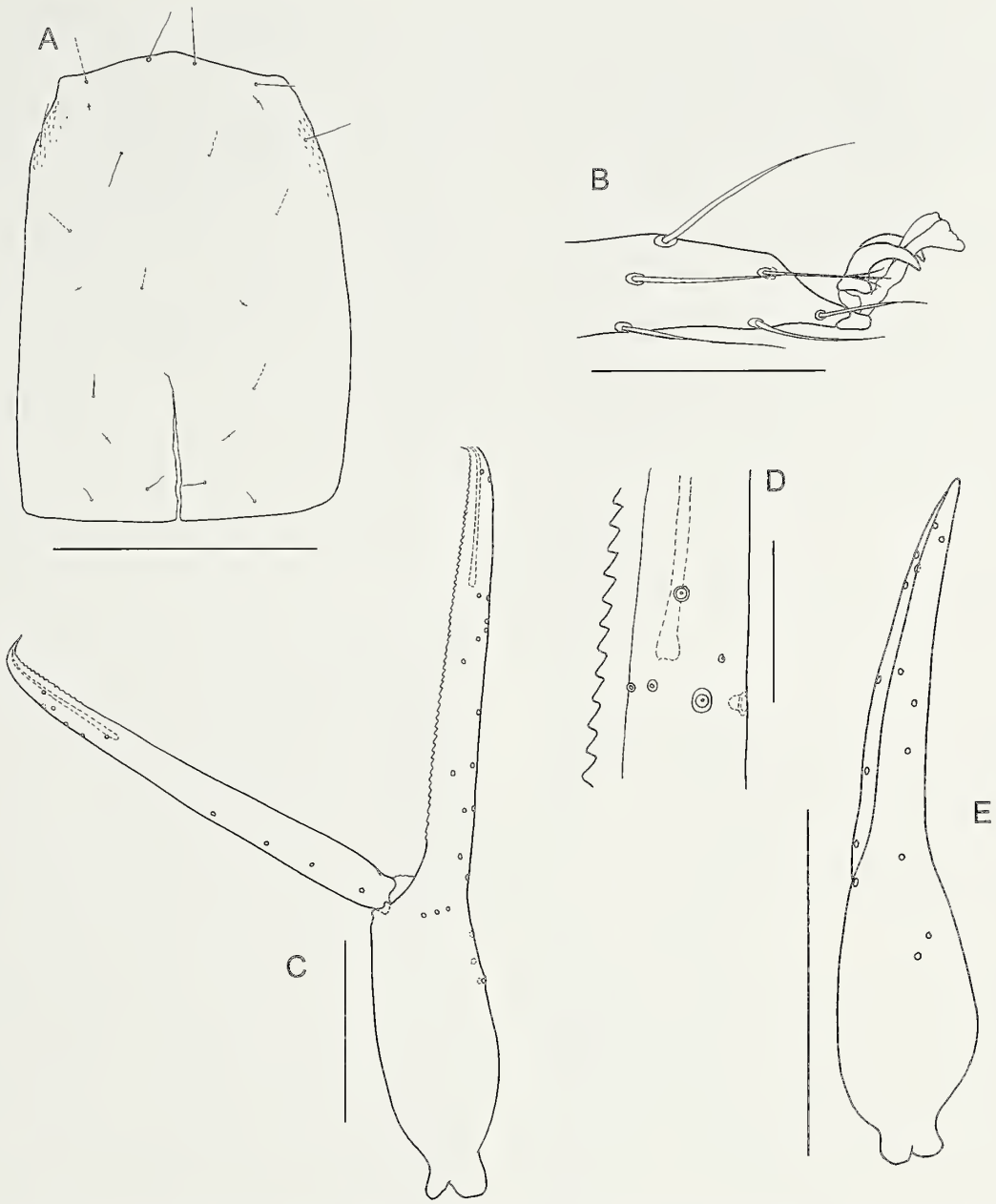

Figure 8.—*Albiorix anophthalmus* Muchmore, male holotype (FSCA, WM7541.01001) unless stated otherwise: A. Carapace, dorsal; B. Tip of left tarsus IV, lateral; C. Left chela, lateral; D. Detail of fixed chelal finger; E. Left chela, setae omitted, dorsal, deutonymph paratype (FSCA, WM7707.01001). Scale lines = 0.5 mm (A, C, E); 0.1 mm (B, D).

1961, L.M. Smith (UCDC); 6 males, 5 tritonymphs, 5 deutonymphs, 1 protonymph, Jardin Botanico Nacional, Viña del Mar (33°00'S, 71°31'W), 16 May 1961, L.M. Smith (UCDC); 1 male, 1 tritonymph, 1 deutonymph, same data (WAM T130757).

Diagnosis.—*Albiorix chilensis* is one of the largest species of the genus, with a chela (without pedicel) length of greater than 1.6 mm. It differs from similarly sized species by the presence of only 20 trichobothria on the fixed chelal finger and hand (Figs. 5B, 9E, 9F), having only 5 setae on the cheliceral hand (Fig. 7B), having 6 setae on the anterior margin of the carapace (Fig. 9B), and the trichobothrium *t* region overlapping with the *est* region (Figs. 5B, 9E, 9F).

Description.—*Adult:* Color: pedipalps and carapace deep red-brown; chelicerae and legs yellow-brown; tergites and sternites pale yellow-brown.

Setae: generally long, straight and acicular.

Chelicera (Fig. 7B): hand with 5 setae; movable finger with 1 subdistal seta; galea very slender and elongate; fixed finger with 9 (male), 10 (female) small teeth; movable finger with 5 (male), 6 (female) teeth; rallum of 4 blades, each with several serrations; lamina exterior absent.

Pedipalp (Fig. 9A): trochanter with scattered granulations, femur and patella lightly granulate on prolateral margin, chelal hand lightly granulate on prolateral surface at base of fingers; trochanter 1.85–2.20 (male), 2.23–2.41 (female), femur

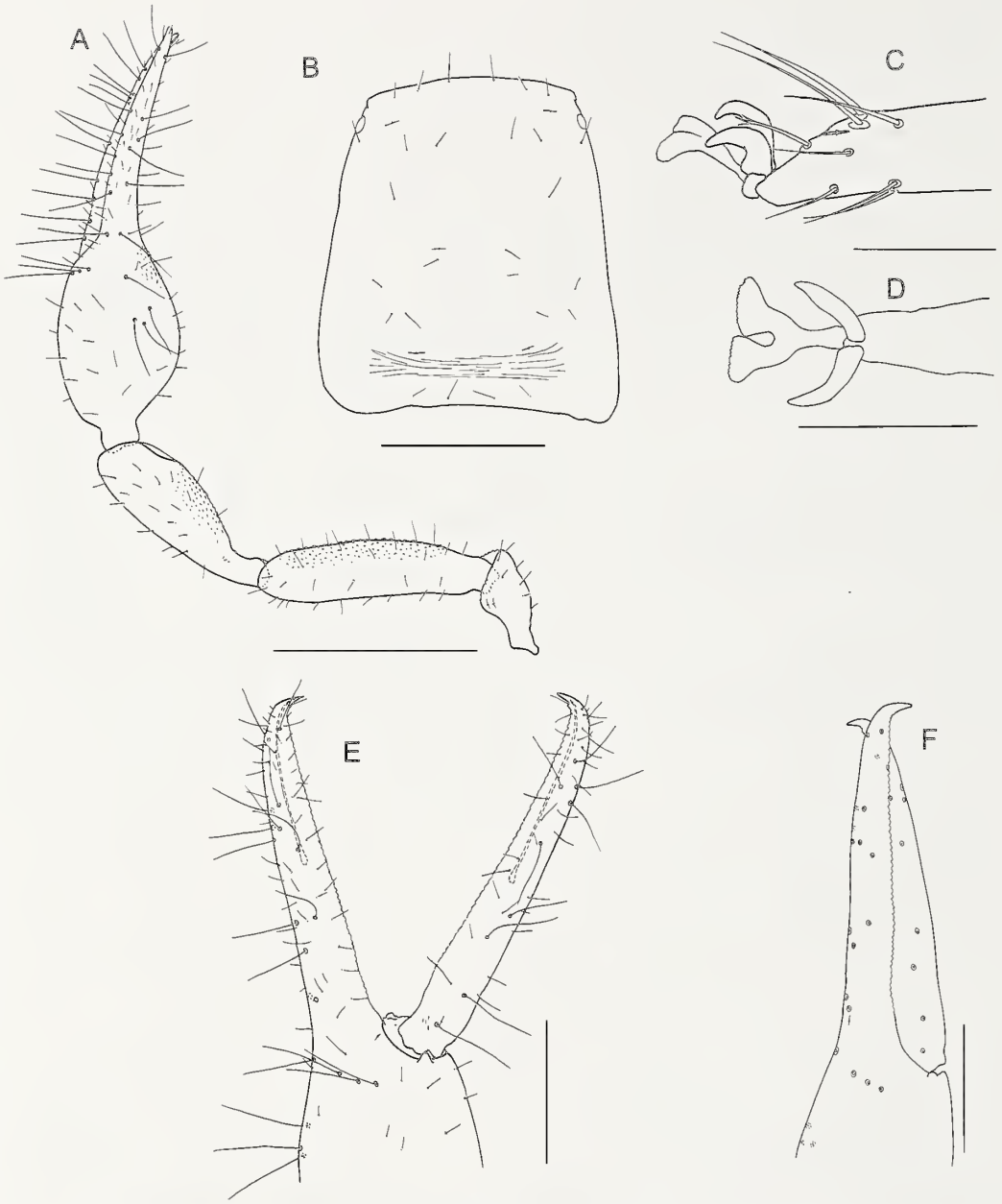

Figure 9.—*Albiorix chilensis* (Ellingsen), specimens from 1 km E. of Maitencillo (UCDC), unless stated otherwise: A. Left pedipalp, dorsal, male; B. Carapace, dorsal; C. Tip of left tarsus IV, lateral, male; D. Tip of left tarsus IV, dorsal, male; E. Right chela, lateral, female; F. Right chela, lateral, holotype female. Scale lines = 1.0 mm (A); 0.5 mm (B, E, F); 0.1 mm (C, D).

4.15–4.35 (male), 4.17–4.55 (female), patella 2.98–3.39 (male), 3.02–3.55 (female), chela (with pedicel) 3.48–3.76 (male), 3.40–3.62 (female), chela (without pedicel) 3.30–3.60 (male), 3.22–3.45 (female), hand (without pedicel) 1.35–1.47 (male), 1.30–1.49 (female) x longer than broad, movable finger 1.49–1.53 (male), 1.40–1.56 (female) x longer than hand (without pedicel). Fixed chelal finger and hand with 20 trichobothria, movable chelal finger with 10 trichobothria (Figs. 4D, 5B, 9E, 9F): *eb*, *esb* and *isb* in straight row at base of finger; *eb*, *esb*, *isb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 4 trichobothria; *ist* region with 5 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus basal to *est* region in fixed finger and basal to *t* region in movable finger. Chelal hand with retrolateral condyle small and rounded. Chelal teeth evenly spaced and juxtadentate: fixed finger with 54 (male), 50 (female) low, retrorse teeth; movable finger with 40 (male), 41 (female) low teeth; base of fixed chelal finger with several small denticles.

Carapace (Fig. 9B): lateral margins evenly convex; 1.25–1.35 (male) 1.32 (female) x longer than broad; with 2 small bulging eyes; with 26 (male), 28 (female) setae including 6 setae on anterior margin and 4 on posterior margin; with very faint posterior furrow situated close to posterior margin.

Coxal region: manducatory process somewhat pointed, with 2 long apical acuminate setae; chaetotaxy 2 + 7: 6: 8: 6: 7 (male); 2 + 7: 6: 9: 7: 7 (female).

Legs: femur + patella 2.43 (male), 2.57 (female) x longer than deep; subterminal tarsal setae deeply bifurcate; arolium longer than claws, deeply divided (Figs. 9C, 9D).

Abdomen: tergites and sternites not divided; sclerites uniseriate. Tergal chaetotaxy: male (1 km E. of Maitencillo), 4: 6: 8: 7: 9: 8: 8: 8: 10: 8 (including 4 tactile setae): 8 (including 4 tactile setae): 2; female (1 km E. of Maitencillo), 4: 6: 8: 8: 9: 10: 10: 10: 8: 8 (including 4 tactile setae): 8 (including 4 tactile setae): 2. Sternal chaetotaxy: male (1 km E. of Maitencillo), 15: (1) 16 [3 + 3] (1): (1) 10 (1): 11: 11: 11: 11: 12: 8: 14 (including 4 tactile setae): 2; female (1 km E. of Maitencillo), 10: (1) 6 (1): (1) 8 (1): 12: 10: 10: 11: 10: 11: 12 (including 4 tactile setae): 2; setae of anterior genital operculum (sternite II) of female very small. Setae of tergites and sternites IX–XI acuminate; with several tactile setae.

Genitalia: male with large dorsal apodeme; median genital sac deeply bipartite; female with large gonosac, which is covered with scattered pores.

Dimensions (mm): Males: male from 1 km E. of Maitencillo followed by other males (where applicable): Body length 3.14 (3.30–3.39). Pedipalp: trochanter 0.538/0.244 (0.458–0.507/0.247–0.251), femur 1.181/0.283 (1.058–1.133/2.50–2.67), patella 1.040/0.347 (0.910–0.957/0.282–0.288), chela (with pedicel) 2.096/0.603 (1.840–1.955/0.494–0.520), chela (without pedicel) 1.992 (1.747–1.845), hand (without pedicel) length 0.816 (0.688–0.736), movable finger length 1.219 (1.056–1.12). Chelicera 0.531/0.264. Carapace 0.994/0.928 (but flattened) (0.939–0.973/0.720–0.760); eye diameter 0.051. Leg I: femur 0.558/0.147, patella 0.288/0.139, tibia 0.438/0.096, metatarsus 0.275/0.077, tarsus 0.307/0.055. Leg IV: femur + patella 0.948/0.390, tibia 0.686/0.179, metatarsus 0.352/0.117, tarsus 0.482/0.073.

Females: holotype followed by other female (where applicable): Body length 4.37. Pedipalp: trochanter 0.635/0.264 (0.638/0.286), femur 1.341/0.295 (1.309/0.314), patella 1.200/0.338 (1.120/0.371), chela (with pedicel) 2.275/0.629 (2.344/0.690), chela (without pedicel) 2.172 (2.224), hand (without pedicel) length 0.936 (0.896), movable finger length 1.312 (1.400). Chelicera 0.631/0.310. Carapace 1.182/0.898 (1.043/1.117, flattened); eye diameter 0.058. Leg I: femur ? (0.605/0.146), patella ? (0.320/0.144), tibia ? (0.498/0.103), metatarsus ? (0.291/0.084), tarsus ? (0.357/0.060). Leg IV: femur + patella ? (1.050/0.406), tibia ? (0.728/0.189), metatarsus ? (0.402/0.129), tarsus ? (0.518/0.081).

Tritonymph: Chelicera: galea long, slightly curved; hand with 5 setae, movable finger with 1 seta; rallum composed of 4 blades, all serrate.

Pedipalp: trochanter 2.14, femur 4.11, patella 3.07, chela (with pedicel) 3.76, chela (without pedicel) 3.56 × longer than broad. Fixed finger with 14 trichobothria, movable finger with 8 trichobothria (Fig. 4C); *eb*, *esb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 3 trichobothria; *ist* region with 3 trichobothria; *est* region with 4 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *st* region with 1 trichobothrium; *t* region with 5 trichobothria; *isb* and *sb* absent. Chelal hand with retrolateral condyle small and rounded.

Carapace: 1 pair of small eyes present; with 24 setae, including 6 setae on anterior margin and 4 setae on posterior margin.

Coxal region: posterior maxillary lyrifissure present, sub-basal.

Legs: much as in adults.

Dimensions (mm): Body length 3.12. Pedipalp: trochanter 0.424/0.198, femur 0.880/0.214, patella 0.728/0.237, chela (with pedicel) 1.544/0.411, chela (without pedicel) 1.464, hand (without pedicel) length 0.568, movable finger length 0.928. Carapace 0.872/0.662.

Deutonymph: Chelicera: galea long, slightly curved; hand with 5 setae, movable finger with 1 seta; rallum composed of 4 blades, all serrate.

Pedipalp: trochanter 1.84, femur 3.27, patella 2.59, chela (with pedicel) 3.56, chela (without pedicel) 3.42 × longer than broad. Fixed finger with 9 trichobothria, movable finger with 6 trichobothria (Fig. 4B); *eb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 2 trichobothria; *ist* region with 2 trichobothria; *est* region with 2 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *t* region with 4 trichobothria. Chelal hand with retrolateral condyle small and rounded.

Carapace: 1 pair of small eyes present; with 20 setae including 6 setae on anterior margin and 4 setae on posterior margin.

Coxal region: posterior maxillary lyrifissure present, sub-basal.

Legs: much as in adult.

Dimensions (mm): Body length 2.26. Pedipalp: trochanter 0.320/0.174, femur 0.609/0.186, patella 0.557/0.215, chela (with pedicel) 1.229/0.345, chela (without pedicel) 1.181, hand (without pedicel) length 0.429, movable finger length 0.750. Carapace 0.634/width not determined.

Protonymph: Chelicera: galea long, nearly straight; hand with 4 setae, movable finger without seta; rallum composed of 4 blades, all serrate.

Pedipalp: trochanter 2.14, femur 3.95, patella 2.93, chela (with pedicel) 3.93, chela (without pedicel) 3.80 × longer than broad. Fixed finger with 3 trichobothria, movable finger with 1 trichobothrium (Fig. 4A); *eb*, *et*, *ist* and *t* present. Chelal hand with retrolateral condyle small and rounded.

Carapace: 1 pair of small eyes present; with 14 setae including 4 setae on anterior margin and 2 setae on posterior margin.

Coxal region: posterior maxillary lyrifissure absent.

Legs: much as in adults.

Dimensions (mm): Body length 1.376. Pedipalp: trochanter 0.218/0.102, femur 0.435/0.110, patella 0.358/0.122, chela (with pedicel) 0.830/0.211, chela (without pedicel) 0.802, hand (without pedicel) length 0.266, movable finger length 0.531. Carapace 0.486/width not determined.

Remarks.—The holotype of *Ideobisium chilense* has been found to be lodged in MZUN and was examined for this study. The specimen is an adult female stored in ethanol and in good condition. The new specimens of *A. chilensis* reported here were collected some 100 km from the type locality of Santiago (Fig. 3D) and are generally in accord with the holotype. Mahnert (1984a) reported a specimen of *Albiorix* from Quebrada de la Plata, Santiago de Chile (33°30′S, 79°55′W), which is located only 25 km from the type locality, that was thought to represent a new species of *Albiorix*. Dr. Mahnert (in litt., June 2013) now confirms that the specimen is more likely to be a specimen of *A. chilensis*.

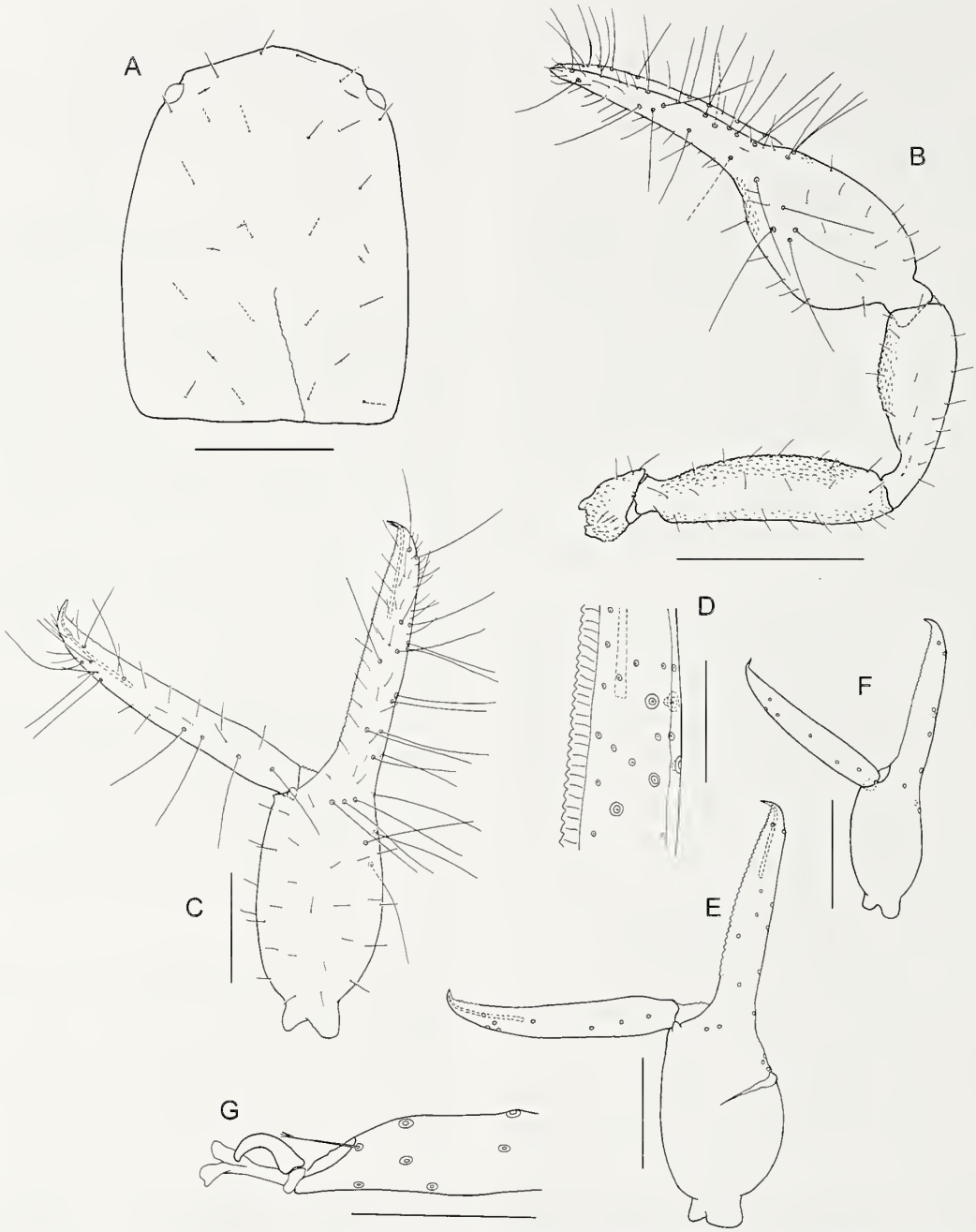

Figure 10.—*Albiorix conodentatus* Hoff, male holotype, unless stated otherwise: A. Carapace, dorsal; B. Right pedipalp, dorsal; C. Left chela, lateral; D. Detail of fixed chelal finger; E. Left chela, lateral, tritonymph (FSCA, WM4776.01006); F. Left chela, lateral, deutonymph (FSCA, WM4776.01007); G. Tip of right tarsus IV, only subterminal tarsal seta shown. Scale lines = 0.5 mm (B); 0.25 mm (A, C, E, F); 0.1 mm (D, G).

Albiorix conodentatus Hoff 1945
Figs. 3C, 10

Albiorix conodentatus Hoff 1945:8–10, Figs. 17–20; Harvey 1991:317; Ceballos 2004:427; Harvey 2013:unpaginated.
Albiorix retrodentatus Hoff: Hoff 1956:25–26 (misidentification).

Material examined.—*Holotype*. Mexico: *Coahuila de Zaragoza*: male, 5 miles W. of Saltillo (25°25′N, 101°05′W), 5 July 1936 [L.I.] Davis (AMNH, Hoff slide S–116.5204).

Other material. Mexico: *Chihuahua*: 1 female, Salaices (27°02′N, 105°13′W), 25 February 1966, J. Reddell, W. Bell (FSCA, WM902.01001); *Coahuila de Zaragoza*: 1 female, Cuatro Ciénegas (Minkley's Camp), Two Cave Canyon, 400 m E. of tip, Sierra San Marcos (26°59′N, 102°05′W), 11 August 1970, roof of small rock shelter, J.J. Landye (FSCA, WM7467.01001); *Nuevo León*: 1 female, near Gruta del Palmito, 7 km SSW. of Bustamante (26°30′N, 100°32′W), no date, Reddell (FSCA, WM974.01001); *Sonora*: 3 males, 3 females, San Miguel de Horcasitas (29°17′N, 110°52′W), no date, Eisen (MCZ, WM4535.01001–6); *Tamaulipas*: 1 female, 10 miles S. of Reynosa (25°55′N, 98°18′W), 6 November 1951, Creighton (AMNH, Hoff slide S–1967). USA: *New Mexico*: 1 male, Eddy County, ca. 14 km NE. of Loving (32°21′N, 103°58′W), 6 September 1991, under rock, dry soil, G. Lowe,

B. Hebert (WAM T127027); 1 male, Eddy County, Whites City (32°11′N, 104°23′W), 24 September 1950, W.J. Gertsch (AMNH, Hoff slide S–1582); 1 male, 1 female, Eddy County, Whites City, boundary Carlsbad Caverns National Park (32°11′N, 104°23′W), 6 September 1991, under rocks, G. Lowe (WAM T127028); *Texas*: 5 males, 2 females, 1 tritonymph, 1 deutonymph, Brewster County, Bullis Gap Range, Honeymoon (29°50′N, 102°37′W), 14 May 1977, C. Solieau (FSCA, WM4776.01001–9); 6 males, 5 females, Brewster County, Bullis Gap Range, ridge top (29°50′N, 102°37′W), 16 May 1977, C. Soileau (WAM T127030); 2 males, Brewster County, Chisos Mountains, Basin (29°16′N, 103°18′W), 28 May 1952, Cazier, Gertsch and Schrammel (AMNH, Hoff slide S–1961.1–2); 1 male, Brewster County, Chisos Mountains, Big Bend National Park (29°16′N, 103°18′W), 28 September 1950, W.J. Gertsch (AMNH, Hoff slide S–1580.2); 1 female, Brewster County, Hot Springs, Big Bend National Park (29°11′N, 103°00′W), 11 September 1950, W.J. Gertseh (AMNH, Hoff slide S–1589.1); 1 female, Hidalgo County, S. of Pharr (26°12′N, 98°11′W), 28 March 1936, S. Mulaik (AMNH, Hoff slide S–211); 1 male, 1 female, Jeff Davis County, Limpia Canyon, Fort Davis (30°47′N, 103°45′W), 27 March 1956, stream bed with ants, E.V. Gregg (AMNH, Hoff slide S–2740.1–2); 1 male, 1 female, Pecos County, 30 miles N. of Sanderson (30°34′N, 102°24′W), 3,450 feet, 5 September 1991, under rocks on slope, G. Lowe, B. Hebert (WAM T127029); 1 male, Terrell County, Sanderson (30°08′N, 102°24′W), 26 May 1952, Cazier, Gertsch and Schrammel (AMNH, Hoff slide S–1964); 7 males, 7 females, Upton County, 7 miles NE. of Crane, McElroy Ranch (31°29′N, 102°18′W), 20 June 1986, D. Sissom, M. Hulsey (FSCA, WM7601); 2 males, 2 females, Val Verde County, 3 miles N. of Langtry (29°51′N, 101°33′W), 3 November 1984, J. Reddell, M. Reyes (FSCA, WM6769); 4 males, 2 females, Val Verde County, rim of Pecos River Canyon, 3 miles from mouth (29°44′N, 101°21′W), 25 June 1947, C.L. Remington (PMNH, WM3326.01001–6); 3 males, 1 female, 1 deutonymph, Val Verde County, Seminole Canyon State Park (29°41′N, 101°19′W), 4 November 1984, J. Reddell (FSCA, WM6768); 1 female, Val Verde County, Shumla (29°47′N, 101°24′W), 26 May 1952, Cazier, Gertsch and Schrammel (AMNH, Hoff slide S–1960.1).

Diagnosis.—*Albiorix conodentatus* differs from other species of the genus by the small, tightly spaced chelal teeth of the fixed chelal finger (Fig. 10D), and the position of trichobothrium est_4 which is situated basally, where it overlaps with the *ist* group.

Description.—*Adult:* Color: pedipalps, carapace and coxal region red-brown; abdomen pale red-brown; ehelicerae and legs light yellow-brown.

Setae: generally long, straight and acicular.

Chelicera: hand with 6 setae, very occasionally 5 or 7 setae; movable finger with 1 subdistal seta; galea very slender and elongate; fixed finger with 4 (male), 4 (female) small teeth; movable finger with 3 (male), 6 (female) teeth; rallum of 4 blades, each with several serrations; lamina exterior absent.

Pedipalp (Fig. 10B): trochanter with seattered granulations on most faces, femur granulate on prolateral and basal region of retrolateral margins, patella finely granulate on prolateral margin, chelal hand very sparsely granulate on prolateral margin at base of fingers; trochanter 2.26–2.54 (male), 2.11–2.47 (female), femur 3.59–4.11 (male), 3.52–4.05 (female), patella 2.60–3.00 (male), 2.41–2.90 (female), chela (with pedicel) 3.29–3.59 (male), 2.92–3.54 (female), chela (without pedicel) 3.14–3.36 (male), 2.81–3.31 (female), hand (without pedicel) 1.35–1.55 (male), 1.31–1.85 (female) x longer than broad, movable finger 1.18–1.40 (male), 1.16–1.37 (female) x longer than hand (without pedicel). Fixed chelal finger and hand with 22 trichobothria, movable chelal finger with 10 trichobothria (Figs. 5C, 10C): *eb*, *esb* and *isb* in straight row at base of finger; *eb*, *esb*, *isb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 5 trichobothria; *ist* region with 6 trichobothria; *est* region with 6 trichobothria, est_4 situated basally, overlapping with *ist* group; *et* slightly distal to *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus basal to *est* region in fixed finger and basal to *t* region in movable finger. Chelal hand with retrolateral eondyle small and rounded. Chelal teeth closely spaced: fixed finger with 44–57 (male), 45–55 (female) closely spaced, triangular retrorse teeth (Fig. 10D); movable finger with several obvious teeth, followed by a series of indistinct very low teeth; base of fixed chelal finger with several small denticles.

Carapace (Fig. 10A): lateral margins evenly convex; 1.16–1.40 (male), 1.12–1.39 (female), x longer than broad; with 2 small bulging eyes; anterior margin medially prominent; with 21–24 (male), 20–24 (female) setae, including 4 (3 in 1 male) on anterior margin and 4 (very rarely 5 or 6) on posterior margin; with very faint posterior furrow situated close to posterior margin.

Coxal region: manducatory process somewhat pointed, with 2 long apical acuminate setae; chaetotaxy 2 + 8: 5: 5: 6: 6 (♂); 2 + 7: 5: 6: 6: 6 (female).

Legs: femur + patella 2.34–2.73 (male), 2.53–2.77 (female) x longer than deep; subterminal tarsal setae trifurcate (Fig. 10G); arolium longer than claws, deeply divided.

Abdomen: tergites not divided, medial sternites without medial suture line; sclerites uniseriate. Tergal chaetotaxy: male, 4: 5: 6: 8: 8: 8: 8: 8: 8: 7 (including 4 tactile setae): 5 (including 3 tactile setae): 2; female, 4: 5: 8: 8: 7: 8: 8: 8: 8: 7: 5 (including 2 tactile setae): 2. Sternal chaetotaxy: male, 9: (1) 13 [3 + 3] (1): (1) 7 (1): 10: 11: 11: 11: 11: 9: 9 (including 4 tactile setae): 2; female, 6: (1) 8 (1): (1) 7 (1): 10: 11: 10: 10: 11: 11: 8 (including 4 tactile setae): 2; setae of anterior genital operculum (sternite II) of female very small. Setae of tergites and sternites IX–XI acuminate; with several tactile setae.

Genitalia: male with small dorsal apodeme; median genital sac deeply bipartite; female with large gonosac which is covered with scattered pores.

Dimensions (mm): Males: holotype followed by other males (where applicable): Body length 2.33 (2.26–2.74). Pedipalp: trochanter ? (damaged)/0.142 (0.323–0.392/0.133–0.170), femur 0.686/0.173 (0.672–0.815/0.174–0.216), patella 0.555/0.201 (0.561–0.665/0.186–0.235), chela (with pedicel) 1.188/0.344 (1.156–1.344/0.321–0.395), chela (without pedicel) 1.116 (1.090–1.265), hand (without pedicel) length 0.477 (0.477–0.585), movable finger length 0.646 (0.608–0.720). Chelicera

0.293/0.149; movable finger length 0.149. Carapace 0.672/0.512 (0.632–0.815/0.494–0.656); eye diameter 0.038. Leg I: femur 0.321/0.091, patella 0.180/0.089, tibia 0.239/0.064, metatarsus 0.149/0.051, tarsus 0.245/0.042. Leg IV: femur + patella 0.557/0.238 (0.525–0.627/0.198–0.250), tibia 0.392/0.097, metatarsus 0.206/0.071, tarsus 0.300/0.034.

Females: specimen from Gruta del Palmito (FSCA, WM974.01001) followed by other females (where applicable): Body length 2.85 (2.63–4.32). Pedipalp: trochanter 0.378/0.160 (0.339–0.467/0.150–0.189), femur 0.800/0.198 (0.682–0.980/0.182–0.248), patella 0.614/0.213 (0.557–0.765/0.202–0.267), chela (with pedicel) 1.402/0.410 (1.179–1.608/0.361–0.475), chela (without pedicel) 1.312 (1.102–1.507), hand (without pedicel) length 0.570 (0.483–0.667), movable finger length 0.736 (0.642–0.864). Chelicera 0.358/0.169. Carapace 0.714/0.585 (but somewhat flattened) (0.627–0.896/0.518–0.720); eye diameter 0.046. Leg I: femur 0.365/0.105, patella 0.186/0.097, tibia 0.276/0.072, metatarsus 0.167/0.055, tarsus 0.246/0.045. Leg IV: femur + patella 0.615/0.243 (0.531–0.752/0.192–0.287), tibia 0.438/0.110, metatarsus 0.242/0.080, tarsus 0.334/0.054.

Tritonymph: Chelicera: galea long, slightly curved; hand with 6 setae, movable finger with 1 seta; rallum composed of 4 blades, all serrate.

Pedipalp: trochanter 2.30, femur 3.58, patella 2.63, chela (with pedicel) 3.43, chela (without pedicel) 3.22 × longer than broad. Fixed finger with 15 trichobothria, movable finger with 8 trichobothria (Fig. 10E); *eb*, *esb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 3 trichobothria; *ist* region with 3 trichobothria; *est* region with 5 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *st* region with 1 trichobothrium; *t* region with 5 trichobothria; *isb* and *sb* absent. Chelal hand with retrolateral condyle small and rounded.

Carapace: anterior margin medially prominent; 1 pair of small eyes present; with 22 setae, including 4 setae on anterior margin and 4 setae on posterior margin.

Coxal region: posterior maxillary lyrifissure present, subbasal.

Legs: much as in adults.

Dimensions (mm): Body length ? (damaged). Pedipalp: trochanter 0.288/0.125, femur 0.572/0.160, patella 0.436/0.166, chela (with pedicel) 0.972/0.283, chela (without pedicel) 0.910, hand (without pedicel) length 0.381, movable finger length 0.544. Carapace 0.559/? (distorted).

Deutonymph: Chelicera: galea long, slightly curved; hand with 5 setae, movable finger with 1 seta; rallum composed of 4 blades, all serrate.

Pedipalp: trochanter 2.03, femur 3.61, patella 2.45, chela (with pedicel) 3.82, chela (without pedicel) 3.64 × longer than broad. Fixed finger with 9 trichobothria, movable finger with 6 trichobothria (Fig. 10F); *eb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 2 trichobothria; *ist* region with 2 trichobothria; *est* region with 2 trichobothria; *et* slightly distal to *it*; *esb* and *isb* absent; *b* region with 2 trichobothria; *t* region with 4 trichobothria; *sb* and *st* absent. Chelal hand with retrolateral condyle small and rounded.

Carapace: anterior margin medially prominent; 1 pair of small eyes present; with 16 setae, including 4 setae on anterior margin and 2 setae on posterior margin.

Coxal region: posterior maxillary lyrifissure present, subbasal.

Legs: much as in adults.

Dimensions (mm): Body length 1.62. Pedipalp: trochanter 0.193/0.095, femur 0.394/0.109, patella 0.282/0.115, chela (with pedicel) 0.688/0.180, chela (without pedicel) 0.688, hand (without pedicel) length 0.256, movable finger length 0.384. Carapace 0.436/0.310.

Remarks.—*Albiorix conodentatus* occurs throughout southern Texas and New Mexico, and northern Mexico (Fig. 3C). Although the label accompanying the slide-mounted holotype of *A. conodentatus* gives the collection site as "Saltillo", the original description by Hoff (1945) gave a more precise location of "5 miles W. of Saltillo". Both the label and publication failed to specify in which state of Mexico the locality was situated. In a series of papers co-authored by the collector (L.I. Davis), it is unequivocally confirmed that the location is situated in the state of Coahuila de Zaragoza (e.g., see Gertsch & Davis 1937, p. 2). Hoff (1956) identified two specimens from Eddy County, New Mexico as *A. retrodentatus*. We have examined one of these specimens (from Whites City, erroneously called White City by Hoff) and found that it conforms very closely to specimens of *A. conodentatus*.

Albiorix edentatus Chamberlin 1930
Figs. 3A, 11

Albiorix edentatus Chamberlin 1930:46–47, figs 1C, 2Y, AA; Chamberlin 1931:figs 28l, 33q; Beier 1932a:173; Roewer 1936:Fig. 30a; Roewer 1937:257; Hoff 1958:15; Harvey 1991:317; Harvey 2013:unpaginated.

Material examined.—*Holotype*. USA: *California*: male, Santa Isabella Creek, east slope of Mt. Hamilton, Santa Clara County (37°21′N, 121°39′W), 18 May 1924, under stones (under large boulders on yellow pine-covered hillside), J.C. Chamberlin (CAS, Entomology Type No. 17457, JC–266.01003).

Paratypes. USA: *California*: 4 tritonymphs, same data as holotype (CAS, JC–266.01001, 2, 4, 5).

Diagnosis.—*Albiorix edentatus* resembles *A. rosario* in having very low teeth of the fixed chelal finger that are much longer than high (Fig. 11D). It differs from *A. rosario* in having trifurcate subterminal tarsal setae (Fig. 11F) and in having trichobothria b_2, *sb* and *st* equidistant from each other (Fig. 11C).

Description.—*Adult:* Color: pedipalps, carapace and coxal region red-brown; abdomen pale red-brown; chelicerae and legs light yellow-brown.

Setae: generally long, straight and acicular.

Chelicera: both chelicerae not present on slide.

Pedipalp (Fig. 11B): trochanter with scattered granulations, especially on retrolateral face, femur and patella lightly granulate on prolateral faces, chelal hand lightly granulate on prolateral surface at base of fingers; trochanter 2.36 (male), femur 4.36 (male), patella 3.23 (male), chela (with pedicel) 3.86 (male), chela (without pedicel) 3.63 (male), hand (without pedicel) 1.44 (male) x longer than broad, movable finger 1.49 (male) x longer than hand (without pedicel). Fixed chelal finger and hand with 21 trichobothria, movable chelal finger with 10 trichobothria (Figs. 5D, 11C): *eb*, *esb* and *isb* in straight row at base of finger; *eb*, *esb*, *isb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 4 trichobothria; *ist* region with 6 trichobothria; *est* region with 6 trichobothria; *et*

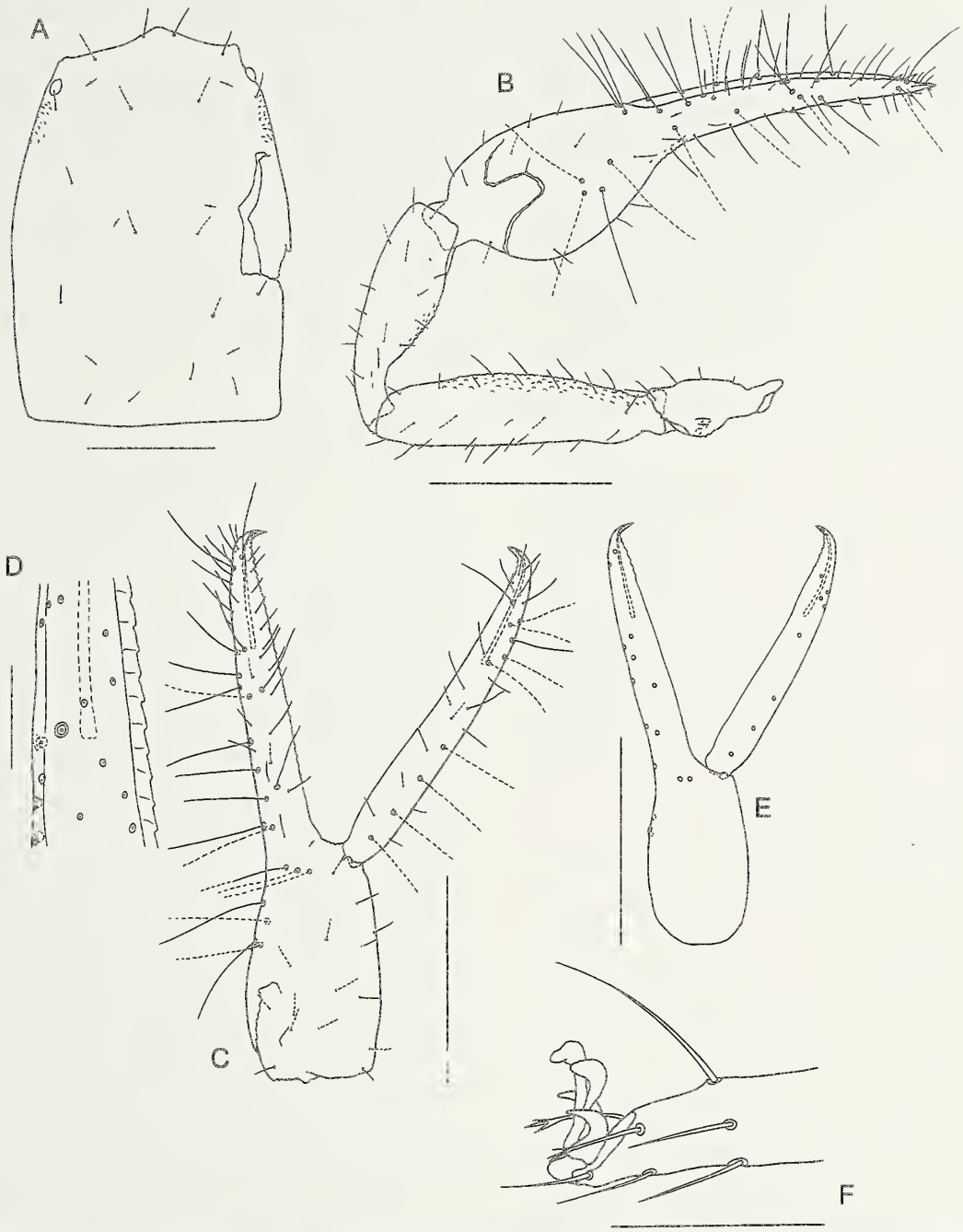

Figure 11.—*Albiorix edentatus* Chamberlin, male holotype, unless stated otherwise: A. Carapace; B. Left pedipalp, dorsal; C. Right chela, lateral; D. Detail of fixed chelal finger; E. Right chela, lateral, tritonymph paratype; F. Tip of right tarsus IV. Scale lines = 0.5 mm (B, C, E); 0.25 mm (A); 0.1 mm (D, F).

slightly distal to *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region; *t* region not overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus at *est* region in fixed finger and base of *t* region in movable finger. Chelal hand with retrolateral condyle small and rounded. Chelal teeth evenly spaced and juxtadentate: fixed finger with 31 (male) very low, retrorse teeth, each much longer than high (Fig. 11D); movable finger with ca. 10 (male) very low, rounded teeth; base of fixed chelal finger with several small denticles.

Carapace (Fig. 11A): lateral margins evenly convex; 1.48 (male) x longer than broad; with 2 small bulging eyes; anterior margin medially prominent; with of 18 (male) setae including 4 setae on anterior margin and 4 on posterior margin; with very faint posterior furrow situated close to posterior margin.

Coxal region: manducatory process somewhat pointed, with 2 long apical acuminate setae; chaetotaxy 2 + 8: 4: 4: 4: 6 (male).

Legs: femur + patella 2.38 (male) x longer than deep; subterminal tarsal setae trifurcate; arolium longer than claws, deeply divided.

Abdomen: tergites and sternites not divided; sclerites uniseriate. Tergal chaetotaxy: male, 4: 5: 6: 6: 6: 6: 6: 6: 6: 6

(including 2 tactile setae): 9 (including 4 tactile setae): 2. Sternal chaetotaxy: male, 8: (1) 9 [3 + 3] (1): (1) 6 (1): 9: 9: 9: 8: 8: 10 (including 2 tactile setae): 6 (including 2 tactile setae): 2. Setae of tergites and sternites IX–XI acuminate; with several tactile setae.

Genitalia: male with small dorsal apodeme; median genital sac bipartite and each arm fairly short.

Dimensions (mm): Males: holotype: Body length not measurable. Pedipalp: trochanter 0.371/0.157, femur 0.824/0.189, patella 0.629/0.195, chela (with pedicel) 1.458/0.378, chela (without pedicel) 1.373, hand (without pedicel) length 0.546, movable finger length 0.816. Chelicera ? (both missing from slide). Carapace 0.784/0.528; eye diameter 0.038. Leg I: femur 0.381/0.102, patella 0.144/0.098, tibia 0.293/0.077, metatarsus 0.102/0.058, tarsus 0.267/0.044. Leg IV: femur + patella 0.632/0.266, tibia 0.461/0.116, metatarsus 0.227/0.083, tarsus 0.332/0.054.

Tritonymph: Chelicera: galea long, slightly curved; hand with 5 setae, movable finger with 1 seta; rallum composed of 4 blades, all serrate.

Pedipalp: trochanter 2.20, femur 4.03, patella 2.77, chela (with pedicel) 3.88, chela (without pedicel) 3.69 × longer than broad. Fixed finger with 15 trichobothria, movable finger with 8 trichobothria (Fig. 11E); *eb*, *esb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 3 trichobothria; *ist* region with 3 trichobothria; *est* region with 5 trichobothria; *et* slightly distal to *it*; *isb* absent; *b* region with 2 trichobothria; *st* region with 1 trichobothrium; *t* region with 5 trichobothria; *sb* absent. Chelal hand with retrolateral condyle small and rounded.

Carapace: anterior margin medially prominent; 1 pair of small eyes present; with 18 setae including 4 setae on anterior margin and 4 setae on posterior margin.

Coxal region: posterior maxillary lyrifissure present, sub-basal.

Legs: much as in adults.

Dimensions (mm): Body length 2.06. Pedipalp: trochanter 0.275/0.125, femur 0.613/0.152, patella 0.446/0.161, chela (with pedicel) 1.093/0.282, chela (without pedicel) 1.040, hand (without pedicel) length 0.397, movable finger length 0.638. Carapace 0.640/? (distorted).

Remarks.—The original meagre description of *A. edentatus* by Chamberlin (1930) was based on the male holotype and four tritonymphs, which he erroneously suggested may have been immature females. The slide-mounted holotype lacks the chelicerae, which were presumably lost during preparation of the specimen.

This species has only been reported from the type locality in central California (Fig. 3A).

Albiorix gertschi Harvey & Muchmore sp. nov.
Figs. 3A, 12

Albiorix mexicanus Chamberlin 1930:45 (in part, specimens from Utah).

Material examined.—*Holotype.* USA: *Utah*: female, Grand County, Moab (38°34′N, 109°33′W), 9 May 1932, W.J. G[ertsch] (CAS, JC–1607.01003).

Paratypes. USA: *Utah*: 1 male, 1 female, collected with holotype (CAS, JC–1607.01001–2); 1 female, Emery County, Ferron (39°06′N, 111°08′W), 23 June 1934, W. Ivie (CAS, JC–1619.02001); 1 male, Emery County, Straight Wash (38°47′N, 110°28′W), 20 April 1928, W.J.G[ertsch] (CAS, JC–449.01001).

Other material. USA: *Arizona*: 2 males, 1 female, Coconino County, Grand Canyon, Colorado River-side, mile 43.2 (36°03′N, 112°09′W), 16–17 October 1982, V. Roth (FSCA, WM7351); 1 male, 1 female, same data (WAM T129657); *Nevada*: 1 male, Pershing County, Lovelock (40°11′N, 118°28′W), 4 May 1941 (MCZ, WM1997.01001).

Diagnosis.—*Albiorix gertschi* closely resembles *A. vigintus* and *A. sarahae* in having trichobothrium ib_5 situated distally (Fig. 12B), but unlike these species which have 20 and 21 trichobothria on the fixed chelal finger and hand, respectively, it has 22 trichobothria (Fig. 12C), with 6 trichobothria in the *ist* group.

Description.—*Adult:* Color: pedipalps, coxae and carapace deep yellow-brown, legs and chelicerae pale yellow-brown.

Setae: generally long, straight and acicular.

Chelicera: hand with 6 setae; movable finger with 1 subdistal seta; galea very slender and elongate; fixed finger with 4 (male), 5 (female) small teeth; movable finger with 6 (male), 5 (female) teeth; rallum of 4 blades, each with several serrations; lamina exterior absent.

Pedipalp (Fig. 12B): trochanter with scattered granulations, femur lightly granulate on prolateral and retrolateral margins, patella lightly granulate on prolateral margin, chelal hand lightly granulate on prolateral surface at base of fingers; trochanter 2.48–2.56 (male), 2.40–2.59 (female), femur 4.57–5.01 (male), 4.31–4.81 (female), patella 3.32–3.85 (male), 2.91–3.48 (female), chela (with pedicel) 3.99–4.47 (male), 3.58–4.45 (female), chela (without pedicel) 3.78–4.24 (male), 3.49–4.23 (female), hand (without pedicel) 1.53–1.64 (male), 1.50–1.66 (female) x longer than broad, movable finger 1.43–1.69 (male), 1.29–1.54 (female) x longer than hand (without pedicel). Fixed chelal finger and hand with 22 trichobothria, movable chelal finger with 10 trichobothria (Figs. 5E, 12C): *eb*, *esb* and *isb* in straight row at base of finger; *eb*, *esb*, *isb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 5 trichobothria, ib_5 displaced distally in advance of *eb*, *esb* and *isb*; *ist* region with 6 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus within *est* region in fixed finger and at base of *t* region in movable finger. Chelal hand with retrolateral condyle small and rounded. Chelal teeth evenly spaced and juxtadentate: fixed finger with 57 (male), 42–47 (female) low, retrorse teeth (Fig. 12D); movable finger with ca. 12–20 (male), ca. 12 (female) obvious, low teeth, followed by additional very low teeth; base of fixed chelal finger with several small dentieles.

Carapace (Fig. 12A): lateral margins evenly convex; with 2 small bulging eyes; anterior margin medially prominent; with 20–23 (male), 20 (female) setae ineluding 4 (5 in 1 male) setae on anterior margin and 4 on posterior margin; with very faint posterior furrow situated close to posterior margin.

Coxal region: manducatory process somewhat pointed, with 2 long apical acuminate setae; chaetotaxy 2 + 7: 5: 6: 5: 6 (male); 2 + 8: 4: 6: 5: 6 (female).

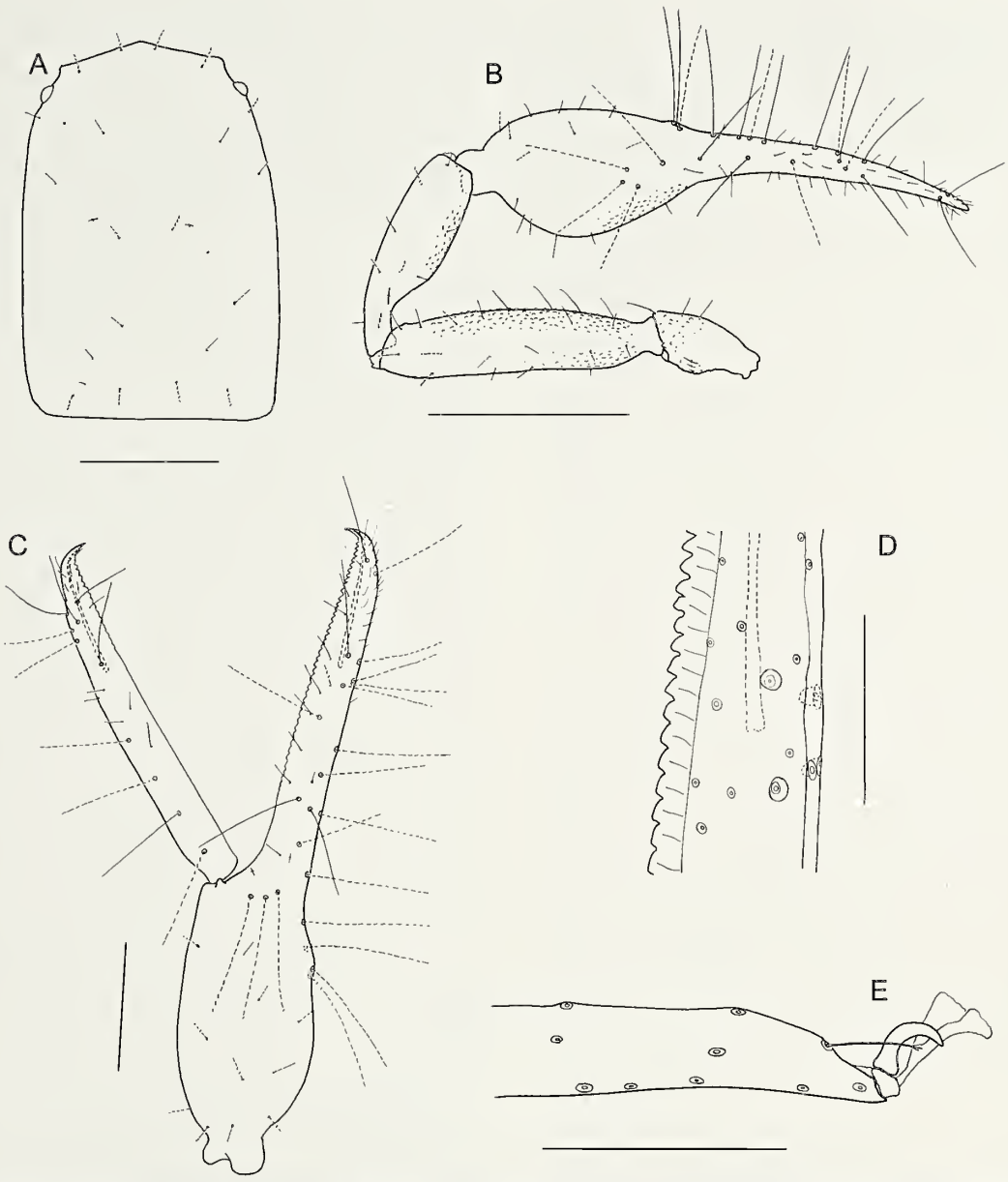

Figure 12.—*Albiorix gertschi* Harvey & Muchmore sp. nov.: female holotype, unless stated otherwise: A. Carapace; B. Left pedipalp, dorsal; C. Left chela, lateral, paratype female (CAS, JC–1607.01002); D. Detail of fixed chelal finger, paratype female (CAS, JC–1607.01002); E. Tip of right tarsus IV, only subterminal tarsal seta shown. Scale lines = 0.5 mm (B); 0.25 mm (A, C); 0.1 mm (D, E).

Legs: femur + patella 2.54 –2.85 (male), 2.82–2.85 (female) x longer than deep; subterminal tarsal setae trifurcate (Fig. 12E); arolium longer than claws, deeply divided.

Abdomen: tergites and sternites not divided; sclerites uniseriate. Tergal chaetotaxy: male, 4: 5: 7: 8: 8: 8: 7: 8: 6: 6 (including 2 tactile setae): 7 (including 4 tactile setae): 2; female, 4: 4: 5: 7: 8: 8: 8: 8: 6: 7 (including 4 tactile setae): 7 (including 4 tactile setae): 2. Sternal chaetotaxy: male, ? (sternite missing): (1) 8 [3 + 3] (1): (1) 7 (1): 10: 8: 9: 8: 8: 6: 6 (including 2 tactile setae): 2; female, 6: (1) 6 (1): (1) 7 (1): 9: 9: 10: 9: 8: 8: 8 (including 4 tactile setae): 2; setae of anterior genital operculum (sternite II) of female very small. Setae of tergites and sternites IX–XI acuminate; with several tactile setae.

Genitalia: male with small dorsal apodeme; median genital sac deeply bifid; female with large gonosac which is covered with scattered pores.

Dimensions (mm): Males: JC–1607.01001 followed by other males (where applicable): Body length 2.06 (2.18–2.32). Pedipalp: trochanter 0.317/0.128 (0.397/0.155–0.156), femur 0.690/0.151 (0.850–0.940/0.179–0.195), patella 0.531/0.160 (0.646–0.730/0.179–0.195), chela (with pedicel) 1.187 (1.456–1.578/0.331–0.378), chela (without pedicel) 1.144 (1.402–1.503), hand (without pedicel) length 0.467 (1.530–1.640), movable finger length 0.669 (0.864–0.948). Chelicera 0.264/0.113; movable finger length 0.113. Carapace 0.640/0.411 (0.779–0.925/0.563–0.602); eye diameter 0.038. Leg I: femur 0.341/0.080, patella 0.167/0.076, tibia 0.260/0.058, metatarsus 0.153/0.045, tarsus 0.250/0.038. Leg IV: femur + patella 0.523/0.198 (0.656–0.672/0.236–0.258), tibia 0.382/0.083, metatarsus 0.186/0.062, tarsus 0.298/0.042.

Females: holotype followed by other females (where applicable): Body length 2.29 (1.94–2.03). Pedipalp: trochanter

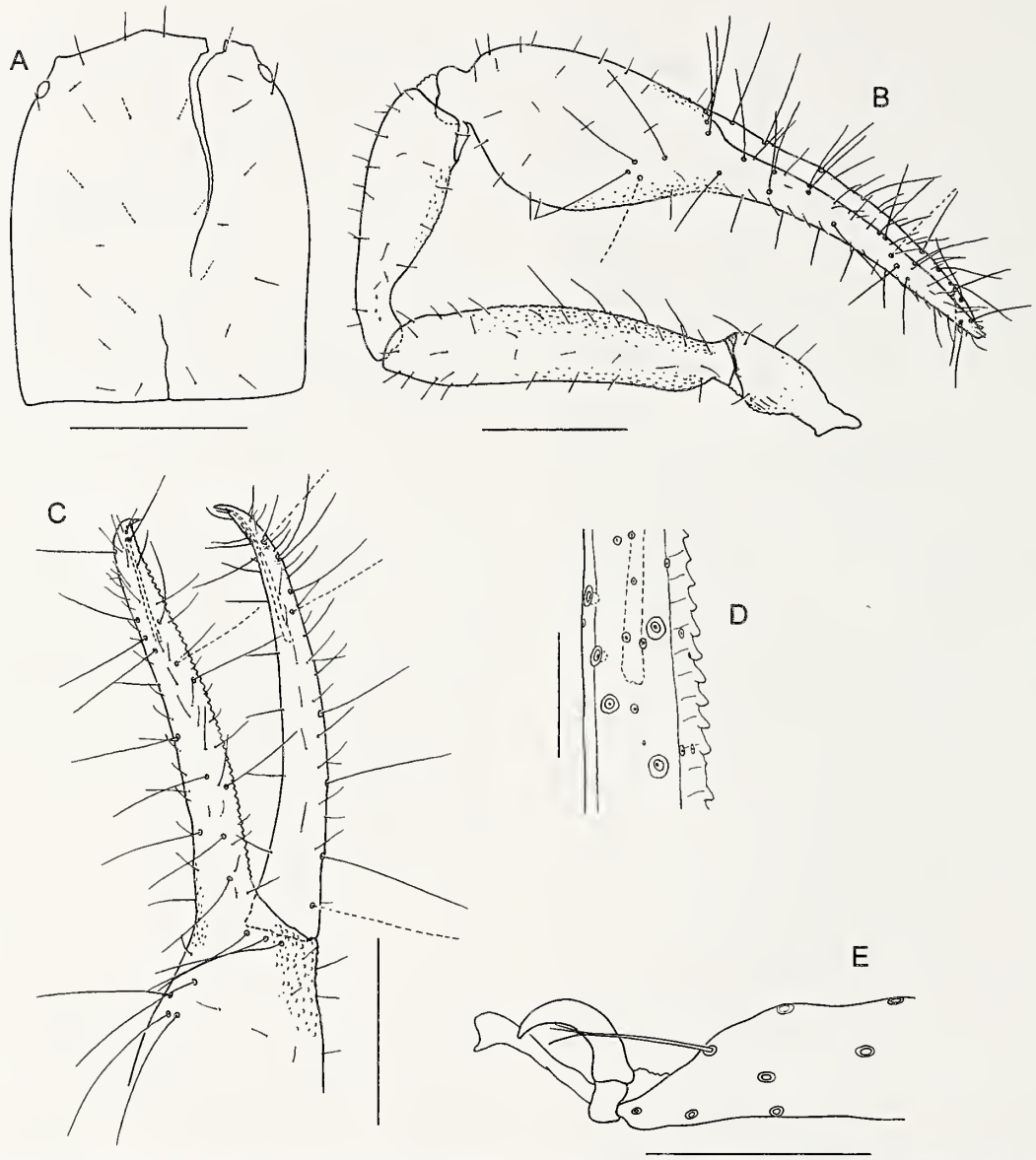

Figure 13.—*Albiorix magnus* Hoff, female holotype: A. Carapace; B. Left pedipalp, dorsal; C. Left chela, lateral; D. Detail of fixed chelal finger; E. Tip of right tarsus IV, only subterminal tarsal seta shown. Scale lines = 0.5 mm (A–C); 0.1 mm (D, E).

0.347/0.134 (0.338–0.384/0.141–0.151), femur 0.726/0.161 (0.736–0.904/0.153–0.191), patella 0.539/0.162 (0.544–0.662/0.162–0.205), chela (with pedicel) 1.267/0.316 (1.280–1.541/0.314–0.371), chela (without pedicel) 1.205 (1.219–1.480), hand (without pedicel) length 0.486 (0.486–0.589), movable finger length 0.720 (0.728–0.885). Chelicera 0.290/0.124; movable finger 0.179. Carapace 0.659/0.475 (0.642–0.762/0.460–0.528); eye diameter 0.038. Leg I: femur 0.352/0.085, patella 0.180/0.077, tibia 0.266/0.060, metatarsus 0.160/0.050, tarsus 0.256/0.038. Leg IV: femur + patella 0.551/0.193 (0.545–0.602/0.193–0.211), tibia 0.411/0.088, metatarsus 0.205/0.063, tarsus 0.314/0.041.

Remarks.—This species is known from desert ecosystems in Utah, Nevada and northern Arizona (Fig. 3A).

Etymology.—This species is named for the late Willis J. Gertsch (1906–1998), former curator of the American Museum of Natural History, New York, and collector of some of the type specimens.

Albiorix magnus Hoff 1945
Figs. 3B, 13

Albiorix magnus Hoff 1945:2–4, figs 1–5; Harvey 1991:317; Ceballos 2004:427; Harvey 2013:unpaginated.
Albiorix aff. *magnus* Hoff: Villegas-Guzman 2006:134.

Material examined.—*Holotype.* MEXICO: *Coahuila de Zaragoza:* female, 20 miles E. of San Pedro (25°45′N, 102°52′W), 5 July 1936, A.M. Davis, L.I. Davis (AMNH, Hoff slide no. S–119.5207).

Diagnosis.—This is one of the largest species of the genus, which differs from others of similar size as follows: from *A. anophthalmus* by the presence of eyes (Fig. 13A); from *A. chilensis* by the presence of 6 setae on the cheliceral hand; from *A. meraculus* by the trifurcate subterminal tarsal seta (Fig. 13E); and from *A. oaxaca* by having fewer and larger teeth on the fixed chelal finger (Fig. 13D).

Description.—*Adult:* Color: pedipalps and carapace deep red-brown; chelicerae and legs yellow-brown; tergites and sternites pale yellow-brown.

Setae: generally long, straight and acicular.

Chelicera: hand with 6 setae; movable finger with 1 subdistal seta; galea very slender and elongate, slightly curved; fixed finger with 9 (female) teeth; movable finger with 6 (female) teeth; rallum of 4 blades, each with several serrations; lamina exterior absent.

Pedipalp (Fig. 13B): trochanter lightly granulate on prolateral and retrolateral faces, femur lightly granulate over most surfaces but with stronger granulations on prolateral face, patella lightly granulate on prolateral face, chela with light granulations on prolateral face, and retrolateral face near base of chelal fingers, and otherwise smooth; trochanter 2.38 (female), femur 4.54 (female), patella 3.36 (female), chela (with pedicel) 3.86 (female), chela (without pedicel) 3.69 (female), hand (without pedicel) 1.51 (female) x longer than broad, movable finger 1.47 (female) x longer than hand (without pedicel). Fixed chelal finger and hand with 22 trichobothria, movable chelal finger with 10 trichobothria (Figs. 5F, 13C): *eb*, *esb* and *isb* in straight row at base of finger; *eb*, *esb*, *isb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 5 trichobothria; *ist* region with 6 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus within *est* region in fixed finger and basal to the *t* region in movable finger. Chelal hand with retrolateral condyle small and rounded. Chelal teeth evenly spaced and juxtadentate: fixed finger with 54 (female) retrorse, close-set teeth (Fig. 13D); movable finger with ca. 9 distal teeth, leading into several very low teeth; base of fixed chelal finger with several small denticles.

Carapace (Fig. 13A): lateral margins evenly convex; 1.23 (female) x longer than broad; with 2 small bulging eyes; anterior margin medially prominent; with 22 setae including 4 setae on anterior margin and 4 on posterior margin; with shallow furrow situated near posterior margin.

Coxal region: manducatory process somewhat pointed, with 2 long apical acuminate setae; chaetotaxy 2 + 9: 6: 7: 7: 7 (female).

Legs: femur + patella 2.78 (female) x longer than deep; metatarsus and tarsus III and IV with sub-basal tactile seta; subterminal tarsal setae trifurcate (Fig. 13E); arolium longer than claws, deeply divided.

Abdomen: tergites and sternites not divided; sclerites uniseriate or nearly so, except for except for female sternite V which has 2 setae not in main row. Tergal chaetotaxy: female, 5: 6: 6: 8: 8: 8: 8: 8: 8: 8 (including 3 tactile setae): 7 (including 4 tactile setae): 2. Sternal chaetotaxy: female, 10: (1) 8 (1): (1) 8 (1): 14: 12: 12: 10: 9: 11: 7 (including 2 tactile setae): 2. Setae of tergites and sternites IX–XI acuminate.

Genitalia: female with large gonosac, which is covered with scattered pores.

Dimensions (mm): Female: holotype: Body length 3.39. Pedipalp: trochanter 0.531/0.223, femur 1.190/0.262, patella 0.947/0.282, chela (with pedicel) 2.048/0.531, chela (without pedicel) 1.960, hand (without pedicel) length 0.804, movable finger length 1.184. Chelicera 0.437/0.204, movable finger length 0.259. Carapace 0.989/0.802; eye diameter 0.051. Leg I: femur 0.560/0.131, patella 0.262/0.122, tibia 0.449/0.083, metatarsus 0.225/0.070, tarsus 0.358/0.052. Leg IV: femur + patella 0.884/0.318, tibia 0.624/0.126, metatarsus 0.353/0.093, tarsus 0.486/0.066.

Remarks.—The right chela of the slide-mounted holotype has been separated from the remainder of the pedipalp, but is not positioned in such a way as to allow the morphology of the chelal teeth to be observed properly. Although the chela is rotated slightly and is dorso-laterally aligned (Fig. 13C), it appears that the teeth of the fixed finger may be basally incised, as in the types of *A. meraculus* (Fig. 14D), as a slight overlap can be observed in many of the teeth. However, both species can be distinguished by the morphology of the subterminal tarsal setae, which are trifurcate in *A. magnus* (Fig. 13E) but are bifurcate *A. meraculus*.

The original description of *A. magnus* by Hoff (1945) gave the type locality as "20 miles E. of San Pedro" even though the label accompanying the slide-mounted holotype simply stated "San Pedro". Hoff (1945) did not specify in which state of Mexico this particular San Pedro was situated, but in a series of papers co-authored by one of the collectors (L.I. Davis), they unequivocally confirm that the location is situated in the state of Coahuila de Zaragoza (e.g., see Gertsch & Davis 1937, p. 2). Villegas-Guzmán (2006) recorded several specimens from Chiapas, Mexico as *Albiorix* affinis *magnus*, but noted discrepancies with the original description by Hoff (1945) and suggested that they may in fact represent an undescribed species. Dr Villegas-Guzmán (in litt.) has kindly reexamined the specimens which are lodged in the Colección Nacional de Arácnidos del Instituto de Biología de la Universidad Nacional Autónoma de México, and confirms that they match the new description of *A. magnus* presented in this manuscript.

Albiorix magnus appears to be widely distributed in Mexico and has been found at the type locality in the state of Coahuila de Zaragoza and in eastern Chiapas near the Guatemalan border (Fig. 3B).

Albiorix meraculus Harvey & Muchmore, sp. nov.
Figs. 3B, 14

Material examined.—*Holotype.* MEXICO: *Jalisco*: Male, Purificación (19°43′N, 104°36′W), 19 November 1941, C. Bolivar (CAS, JC–1658.01001).

Paratype. MEXICO: *Jalisco*: 1 tritonymph, same data as holotype (CAS, JC–1658.01002).

Diagnosis.—*Albiorix meraculus* is one of the largest species of *Albiorix*, with a chela length (with pedicel) of 2.032 mm (male). It differs from other species of the genus by the morphology of the teeth on the fixed chelal finger, most of which are deeply incised basally forming an overhanging ridge. In addition, the subterminal tarsal seta is bifurcate and each tine is quite long.

Description.—*Adult:* Color: pedipalps and carapace deep red-brown; chelicerae and legs yellow-brown; tergites and sternites pale yellow-brown.

Setae: generally long, straight and acicular.

Chelicera: hand with 6 setae; movable finger with 1 subdistal seta; galea very slender and elongate, slightly curved;

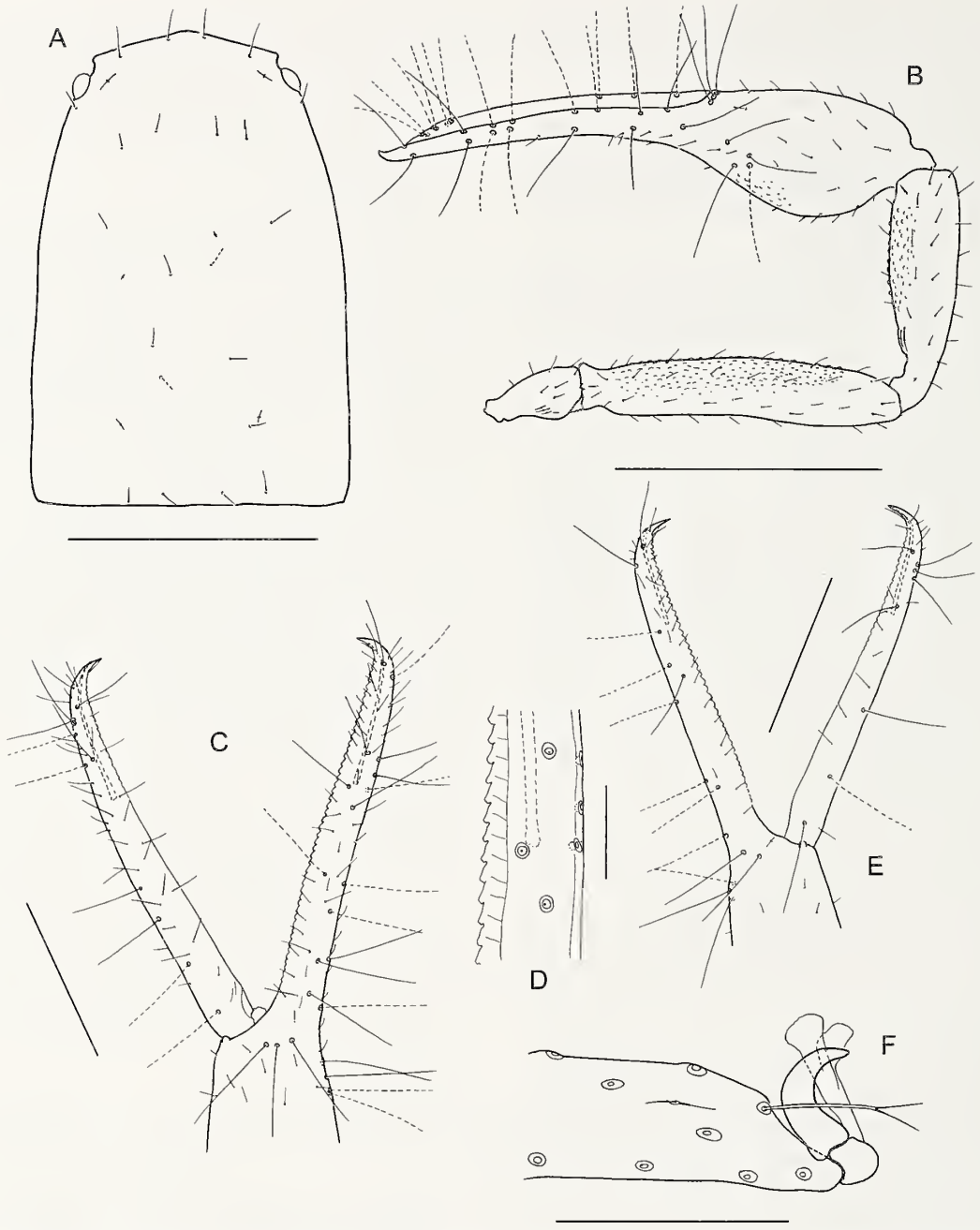

Figure 14.—*Albiorix meraculus* Harvey & Muchmore sp. nov., male holotype, unless stated otherwise: A. Carapace, dorsal; B. Right pedipalp, dorsal; C. Left chela, lateral; D. Detail of fixed chelal finger; E. Right chela, lateral, tritonymph paratype (CAS, JC–1658.01002); F. Tip of right tarsus IV, only subterminal tarsal seta shown. Scale lines = 1.0 mm (B); 0.5 mm (A, C, E); 0.1 mm (D, F).

fixed finger with 6 small teeth as well as several minute teeth; movable finger with 4 teeth; rallum of 4 blades, each with several serrations; lamina exterior absent.

Pedipalp (Fig. 14B): trochanter lightly granulate on retrolateral face, femur lightly granulate over most surfaces, patella lightly granulate over prolateral face, chela fairly smooth; femur 5.25 (male), patella 3.51 (male), chela (with pedicel) 4.49 (male), chela (without pedicel) 4.34 (male), hand (without pedicel) 1.62 (male) x longer than broad, movable finger 1.64 (male) x longer than hand (without pedieel). Fixed chelal finger and hand with 22 trichobothria, movable chelal finger with 10 trichobothria (Fig. 14C): *eb*, *esb* and *isb* in straight row at base of finger; *eb*, *esb*, *isb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 4 trichobothria; *ist* region with 7 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus near *est* region in fixed finger and basal to the *t* region in movable finger. Chelal hand with retrolateral condyle small and rounded. Chelal teeth evenly spaced and juxtadentate: fixed finger with 58 (male) strongly retrorse teeth, margins of most

teeth deeply dissected basally forming an overhanging ridge; movable finger with several distal teeth none of which are upraised, leading into many very low teeth which extend along entire length of finger; base of fixed chelal finger with several small denticles.

Carapace (Fig. 14A): lateral margins evenly convex; 1.47 (male) x longer than broad; with 2 small bulging eyes; anterior margin medially prominent; with 22 setae including 4 setae on anterior margin and 4 on posterior margin; without furrows.

Coxal region: manducatory process somewhat pointed, with 2 long apical acuminate setae; chaetotaxy 2 + 8: 8: 7: 8: 9 (male).

Legs: femur + patella 2.53 (male) x longer than deep; metatarsus and tarsus III and IV with sub-basal tactile seta; subterminal tarsal setae bifurcate with long tines (Fig. 14F); arolium longer than claws, deeply divided (Fig. 14F).

Abdomen: tergites and sternites not divided, except for sternite III, which is medially divided; sclerites uniseriate, except for sternites II and III, which have the setae somewhat scattered. Tergal chaetotaxy, male: 4: 6: 6: 8: 8: 8: 10: 8: 8: 8 (including 2 lateral tactile setae): 9 (including 4 tactile setae): 2. Sternal chaetotaxy, male: 15: (1) 18 [2 + 3] (1): (1) 9 (1): 10: 13: 9: 11: 11: 11: 9 (including 4 tactile setae): 3. Setae of tergites and sternites IX–XI acuminate.

Genitalia: male with small dorsal apodeme; median genital sac bipartite and each arm fairly short.

Dimensions (mm): Male: holotype (JC–1658.01001): Body length ca. 3.12. Pedipalp: trochanter ? (damaged)/0.193, femur 1.192/0.227, patella 0.898/0.256, chela (with pedicel) 2.032/0.453, chela (without pedicel) 1.968, hand (without pedicel) length 0.736, movable finger length 1.208. Chelicera 0.368/0.158, movable finger length 0.224. Carapace 0.960/0.651; eye diameter 0.061. Leg I: femur 0.560/0.126, patella 0.264/0.109, tibia 0.447/0.083, metatarsus 0.231/0.064, tarsus 0.371/0.046. Leg IV: femur + patella 0.909/0.359, tibia 0.650/0.136, metatarsus 0.325/0.097, tarsus 0.466/0.061.

Tritonymph: Chelicera: galea long, slightly curved; hand with 6 setae, movable finger with 1 seta; fixed finger with 6 small teeth, movable finger with 3 small teeth; rallum composed of 4 blades, all serrate.

Carapace: anterior margin medially prominent; 1 pair of rounded eyes present; with 22 setae including 4 setae on anterior margin and 4 setae on posterior margin.

Pedipalp: trochanter 2.24, femur 5.27, patella 3.54, chela (with pedicel) 4.57, chela (without pedicel) 4.40, hand (without pedicel) 1.61 × longer than broad; movable finger 1.69 × longer than hand (without pedicel). Fixed finger with 14 trichobothria, movable finger with 8 trichobothria (Fig. 14E); *eb*, *esb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 3 trichobothria; *ist* region with 3 trichobothria; *est* region with 4 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *st* region with 1 trichobothrium; *t* region with 5 trichobothria. Chelal hand with retrolateral eondyle small and rounded.

Legs: much as in adult.

Dimensions (mm): Body length ca. 2.92. Pedipalp: trochanter 0.358/0.160, femur 0.944/0.179, patella 0.658/0.186, chela (with pedicel) 1.563/0.342, chela (without pedicel) 1.504, hand (without pedicel) length 0.550, movable finger length 0.928. Carapace 0.726/0.517.

Remarks.—*Albiorix meraculus* is known only from two specimens collected in the southern Mexican state of Jalisco (Fig. 3B). It is one of the largest species of the genus, and comparable in size to *A. anophthalmus*, *A. chilensis*, *A. magnus* and *A. oaxaca*. It is easily distinguished from these species by the unusual morphology of the teeth of the fixed chelal finger, which are strongly incised basally (Fig. 14D).

Etymology.—The speeific epithet refers to the type locality, Purificación; *meraculus*, a Latin diminutive meaning pure, unadulterated, genuine (Brown 1956).

Albiorix mexicanus (Banks 1898)
Figs. 3B, 6A, 7A, 7C, 7D, 15

Ideoroncus mexicanus Banks 1898:289; Chamberlin 1923:359–360, plate 2 Fig. 13, plate 3 Figs. 14, 34.

Albiorix mexicanus (Banks): Chamberlin 1930:45 Figs. 2f, 2dd; Chamberlin 1931:Figs. 9j, 11u, 17q, 19g, 25l, 59; Beier 1932a:173; Beier 1932b:Fig. 255; Roewer 1936:Fig. 30c; Roewer 1937:257, Fig. 215; Vachon 1949:Fig. 203f; Hoff 1958:14; Mahnert 1984a:673–675, fig 42; Harvey 1991:317; Ceballos 2004:427–428; Harvey & Volschenk 2007:368, Figs. 1–4; Harvey 2013:unpaginated.

Not *Ideoroncus mexicanus* Banks: With 1905:127–131, plate 9 Figs. 2a–d, plate 10 Figs. 1a–f (misidentification; *Bochica witli* (Chamberlin)).

Material examined.—*Neotype.* MEXICO: *Baja California Norte*: female, Bahía de Las Ánimas (labelled "Las Animas Bay") (28°50′N, 113°20′W), 8 May 1923, under stone, J.C. Chamberlin (CAS, Entomology Type No. 1267, JC–370.01001; slide).

Other material. MEXICO: *Baja California Norte:* 1 tritonymph, Isla San Esteban (28°42′N, 112°36′W), 20 April 1921, sifted from mesquite leaves, J.C. Chamberlin (CAS, JC–110.01001; 2 slides); *Baja California Sur*: 1 tritonymph, Isla San Marcos (27°13′N, 112°06′W) (CAS, JC–371.01001).

Diagnosis.—*Albiorix mexicanus* differs from other species of the genus by the sharply pointed teeth of the fixed chelal finger (Fig. 15C).

Description.—*Adult:* Color: uniformly pale yellow-brown (neotype; KOH treated).

Setae: generally long, straight and acicular.

Chelicera (Fig. 7A): hand with 5 setae; movable finger with 1 subdistal seta; galea very slender and elongate; fixed finger with 8 (female) small, sub-equal teeth; movable finger with 4 (female) small teeth; rallum of 4 blades, each with several serrations; lamina exterior absent.

Pedipalp (Fig. 15A): trochanter and femur entirely granulate, patella lightly granulate on prolateral margin, chelal hand lightly granulate on prolateral and retrolateral faces at base of fingers; trochanter 2.46 (female), femur 4.48 (female), patella 3.04 (female), chela (with pedicel) 3.70 (female), chela (without pedicel) 3.51 (female), hand (without pedicel) 1.34 (female) x longer than broad, movable finger 1.62 (female) x longer than hand (without pedicel). Fixed chelal finger and hand with 20 trichobothria, movable chelal finger with 10 trichobothria (Fig. 15A): *eb*, *esb* and *isb* in straight row at base of finger; *eb*, *esb*, *isb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 4 trichobothria; *ist* region with 5 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t*

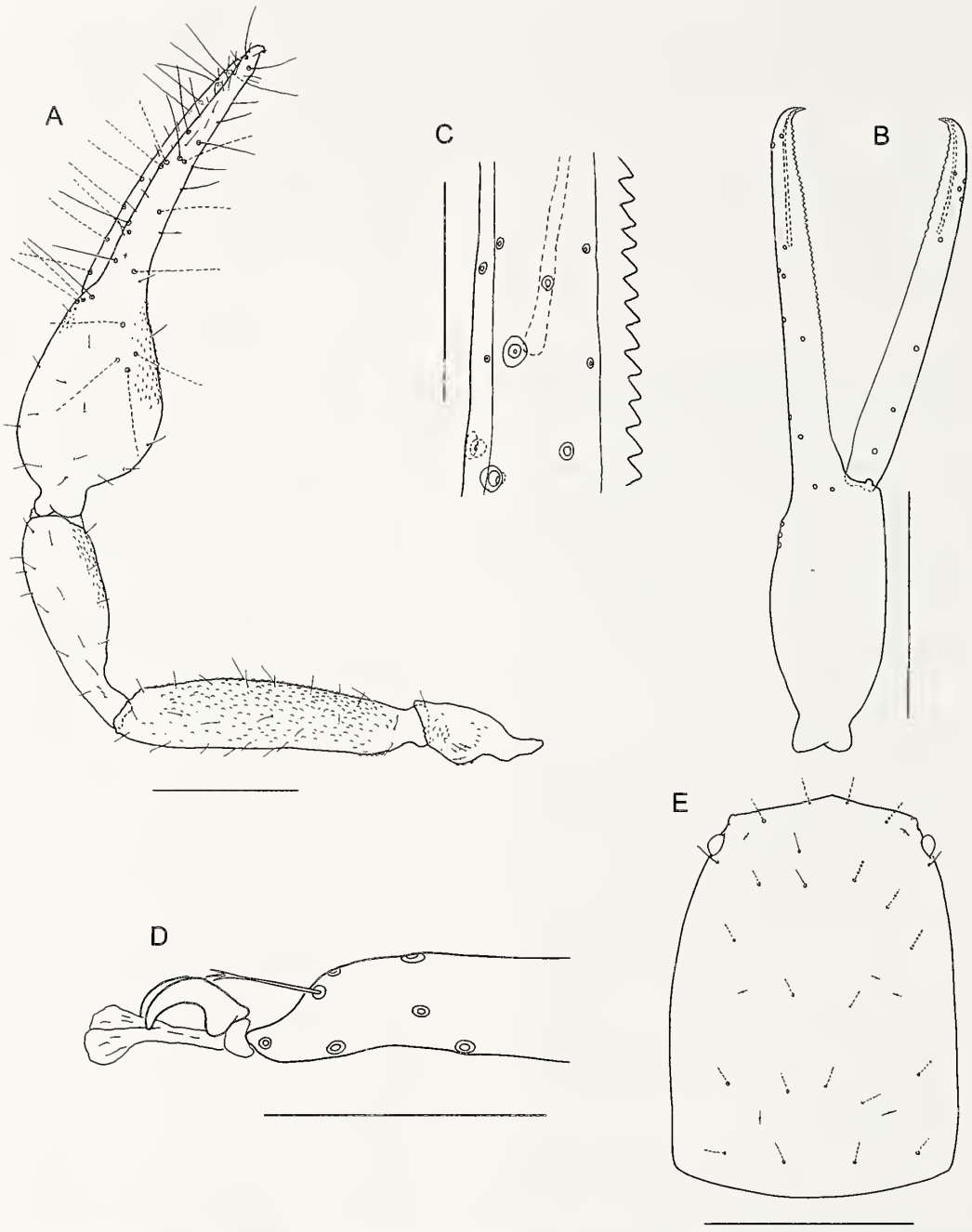

Figure 15.—*Albiorix mexicanus* (Banks): female neotype (CAS) unless stated otherwise: A. Left pedipalp, dorsal; B. Right chela, lateral, tritonymph (CAS, JC–110.01001); C. Detail of fixed chelal finger, tritonymph (CAS, JC–110.01001); D. Tip of right tarsus IV, only subterminal tarsal seta shown; E. Carapace, dorsal. Scale lines = 0.5 mm (A, B, E); 0.1 mm (C, D).

region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus within *est* region in fixed finger and basal to *t* region in movable finger. Chelal hand with retrolateral condyle small and rounded. Chelal teeth evenly spaced and juxtadentate: fixed finger with ca. 69 (female) teeth; movable finger with ca. 30 (female) teeth; shape not discernible due to poor orientation; base of fixed chelal finger with several small denticles.

Carapace (Fig. 15E): lateral margins evenly convex; with 2 small bulging eyes; anterior margin medially straight; with 24 setae including 4 setae on anterior margin and 4 on posterior margin; with very faint posterior furrow situated close to posterior margin.

Coxal region: manducatory process somewhat pointed, with 2 long apical acuminate setae; chaetotaxy 2 + 7: 5: 5: 6: 5 (female).

Legs: femur + patella 2.62 (female) x longer than deep; subterminal tarsal setae trifurcate (Fig. 15D); arolium longer than claws, deeply divided (Fig. 15D).

Abdomen: tergites not divided, medial sternites without medial suture line; sclerites uniseriate. Tergal chaetotaxy: female, 4: 4: 4: 6: 7: 7: 8: 7: 6: 7 (including 2 tactile setae): 5

(including 2 tactile setae): 2. Sternal chaetotaxy: ♀, 6: (1) 6 (1): (1) 6 (1): 8: 10: 9: 9: 10: 10: 7 (including 3 tactile setae): 2; setae of anterior genital operculum (sternite II) of female very small. Setae of tergites and sternites IX–XI acuminate; with several tactile setae.

Genitalia: female with large gonosac, which is covered with scattered pores.

Dimensions (mm): Female: neotype: Body length ca. 2.53. Pedipalp: trochanter 0.394/0.160, femur 0.896/0.200, patella 0.656/0.216, chela (with pedicel) 1.504/0.407, chela (without pedicel) 1.428, hand (without pedicel) length 0.547, movable finger length 0.884. Chelicera 0.337/0.152. Carapace 0.819/0.598; eye diameter 0.051. Leg I: femur 0.411/0.095, patella 0.191/0.188, tibia 0.312/0.064, metatarsus 0.173/0.051, tarsus 0.250/0.038. Leg IV: femur + patella 0.674/0.257, tibia 0.460/0.099, metatarsus 0.238/0.070, tarsus 0.347/0.051.

Tritonymph: Chelicera: galea long, slightly curved; hand with 6 setae, movable finger with 1 seta; fixed finger with 6 small teeth, movable finger with 4 small teeth; rallum composed of 4 blades, all serrate.

Carapace: anterior margin medially prominent; 1 pair of rounded eyes present; with 21 setae including 4 setae on anterior margin and 4 setae on posterior margin.

Pedipalp: trochanter 2.35, femur 4.63, patella 3.46, chela (with pedicel) 4.03, chela (without pedicel) 3.88, hand (without pedicel) 1.44 × longer than broad; movable finger 1.65 × longer than hand (without pedicel). Fixed finger with 14 trichobothria, movable finger with 8 trichobothria (Fig. 15B); *eb*, *esb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 3 trichobothria; *ist* region with 3 trichobothria; *est* region with 4 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *st* region with 1 trichobothrium; *t* region with 5 trichobothria. Chelal hand with retrolateral condyle small and rounded.

Legs: much as in adult.

Dimensions (mm): Body length ca. 2.86. Pedipalp: trochanter 0.369/0.157, femur 0.862/0.186, patella 0.640/0.185, chela (with pedicel) 1.443/0.358, chela (without pedicel) 1.380, hand (without pedicel) length 0.514, movable finger length 0.848. Carapace 0.720/0.550.

Remarks.—The original description of *Ideoroncus mexicanus* by Banks (1898) specifically mentioned only a single specimen collected from San Miguel de Horcasitas, situated in the state of Sonora, Mexico. This specimen was lodged in the California Academy of Sciences but was destroyed in 1906 during the San Francisco earthquake and resulting fire (Chamberlin 1923). A neotype specimen from Baja California was subsequently nominated by Chamberlin (1923). This specimen was collected from Bahía de Las Ánimas in Baja California Sur and is lodged in the California Academy of Sciences. Although Banks (1898) specifically stated that he had examined only a single specimen of *I. mexicanus*, we have found several specimens collected by G. Eisen from San Miguel de Horcasitas, apparently from March to May 1892 (Eisen 1895), which are likely to be conspecific with the destroyed holotype. These specimens are lodged in the Museum of Comparative Zoology and bear the label "*Ideoroncus angustus* Banks" a name that has never been published by Banks or any other author. They consist of three males and three females that have been mounted on microscope slides by W.B. Muchmore, and which clearly represent specimens of *A. conodentatus*. Because they are not labelled with the name *I. mexicanus* and were not mentioned in the original description of *I. mexicanus*, they can be clearly disregarded as part of the type series (International Commission on Zoological Nomenclature 1999). As noted by Mahnert (1984a), these specimens differ from the neotype of *A. mexicanus* in the number of trichobothria on the fixed finger (they have a total of 22, including an extra trichobothrium in each of the *ib* and *ist* groups, compared with the 20 trichobothria found in *A. mexicanus*) and have quite differently shaped chelal teeth. Because these specimens bear no type status, the fact that the original type specimen and the neotype belong to different species has no relevance to this situation (International Commission on Zoological Nomenclature 1999, Article 75) and we here base our concept of *A. mexicanus* on the neotype designated by Chamberlin (1923).

Chamberlin (1923) listed only the female neotype in his redescription of *Ideoroncus mexicanus*, but also referred to two other specimens without providing any collection data. Among the Chamberlin collection lodged in CAS is a specimen from Isla San Esteban (JC–110.01001) which is labelled as a female 'neoparatype' by Chamberlin, and later listed among the material identified as *A. mexicanus* by Chamberlin (1930). This specimen is in fact a tritonymph and likely to be correctly associated with *A. mexicanus* due to the reduced number of trichobothria, 14, on the fixed chelal finger and hand which is characteristic of *Albiorix* tritonymphs with an adult configuration of 20 trichobothria. These locations are only 75 km apart in the Gulf of California. The third specimen is likely to have been from Isla San Marcos, which likewise was claimed to be a female by Chamberlin (1930) but is also a tritonymph and is labelled as a 'neoparatype'. Unlike the tritonymph from Isla San Esteban, the nymph from Isla San Marcos has 15 trichobothria on the fixed chelal finger and hand, suggesting it may represent a different species. Adult specimens from this locality are required to establish its identity. Although W.B. Muchmore was able to examine this second specimen in 1994, the specimen can no longer be found in CAS, and a more detailed examination has not been possible.

The neotype is mounted on a microscope slide, but only left leg I and right leg IV are dissected from the body. The remaining appendages remain attached and although it is possible to count the number of chelal teeth, as they are visible through the cleared fingers, it is not possible to observe their morphology. This is highly regrettable as the shape of the chelal teeth is an extremely important factor in assisting to delimit species of *Albiorix*. As discussed above, the female neotype has a reduced trichobothrial number with only 20 trichobothria on the fixed chelal finger and hand (Fig. 15A). Comparisons with other ideoroncid species suggest that a tritonymph of a species with this pattern would be expected to have 14 trichobothria (Harvey et al. 2007; Mahnert 1984a). This feature is indeed found in the tritonymph collected from Isla San Esteban which is situated only 75 km from the type locality. The teeth of the fixed chelal finger of this tritonymph are clearly quite sharply pointed (Fig. 15C), in contrast to the slightly rounded tips of the teeth in *A. parvidentatus*. It is not

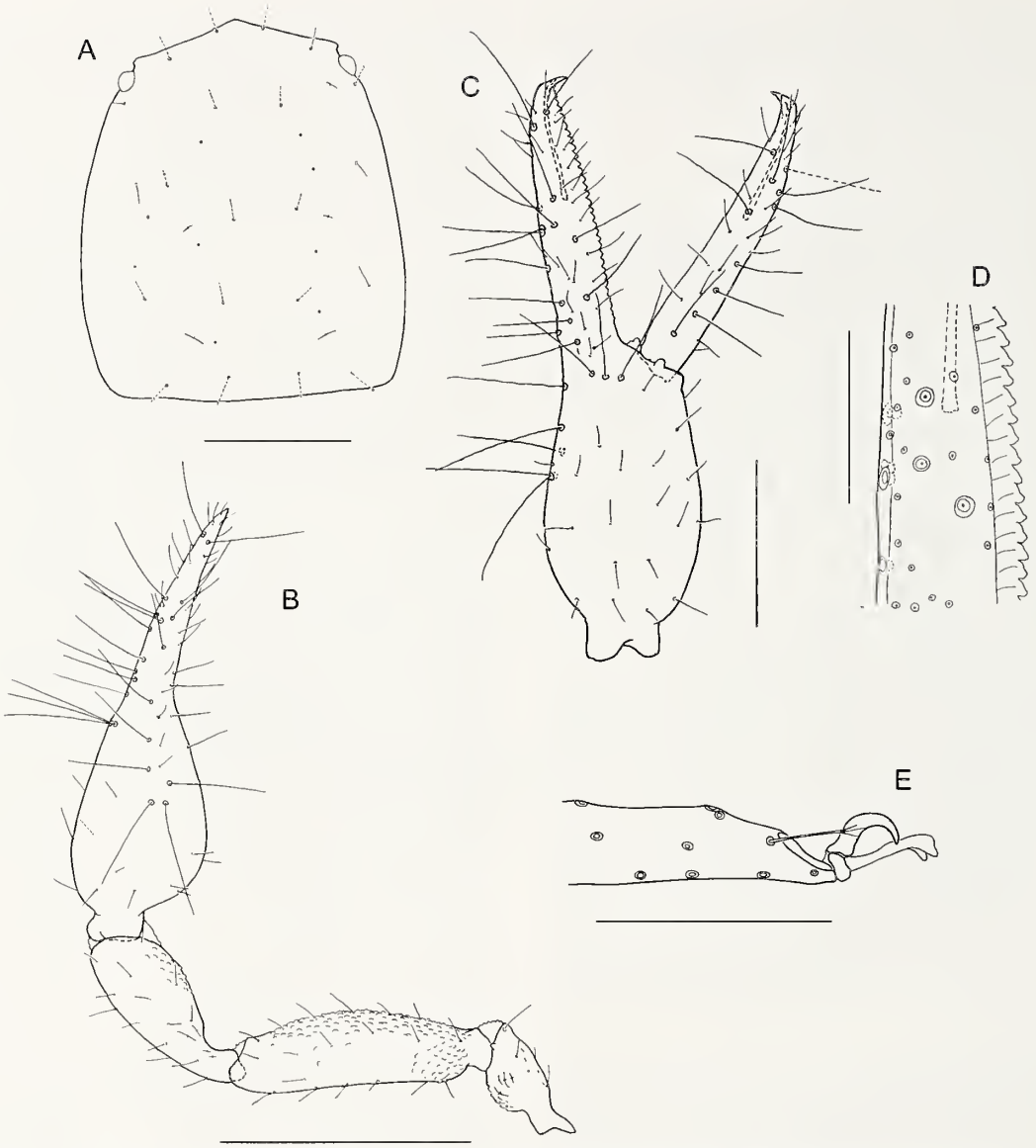

Figure 16.—*Albiorix minor* Harvey & Muchmore sp. nov., male holotype (FSCA, WM1244.01004): A. Carapace; B. Left pedipalp, dorsal; C. Right chela, lateral; D. Detail of fixed chelal finger; E. Tip of left tarsus IV, only subterminal tarsal seta shown. Scale lines = 0.5 mm (B); 0.2 mm (A); 0.25 mm (C); 0.1 mm (D–F).

known for certain whether the neotype also has sharply pointed teeth, but we prefer to assume that this is the case until it can be proven otherwise by the study of new specimens from the type locality.

The other specimens identified as *A. mexicanus* by Chamberlin (1930) belong to other species: a female from El Centro, California (JC–375.02001), belongs to *A. parvidentatus*; the female from Saint George, Utah (JC–245.01001) is assigned to *A. vigintus*; a male from a series of 8 adults from Straight Wash, Utah (JC–449.01001-8) was examined (the other seven specimens were not located for this study) and identified as *A. gertschi*. The other specimens listed by Chamberlin (1930), a male from Straight Canyon, San Rafael Desert, Utah (JC–450.01001) and a female from Bluff, Utah (JC–437.01001) were not located for this study.

Albiorix mexicanus has been recorded from only a small area of Baja California, Mexico (Fig. 3B).

Albiorix minor Harvey & Muchmore, sp. nov.
Figs. 3B, 16

Material examined.—*Holotype*. MEXICO: *Querétaro*: male, 1 mile SW. of Río Blanco, (21°12′N, 99°45′W), 8 July 1967, under rock in field (FSCA, WM1244.01004).

Paratypes. MEXICO: *Querétaro*: 5 males, 1 female, collected with holotype (FSCA, WM1244.01001–3, 5, 6); 1 male, collected with holotype (WAM T129658, WM1244.01007); *Hidalgo*: 1 female, 10–20 miles S. of Jacala, (20°47′N, 99°11′W), 20 July 1956, V. Roth and W. Gertsch (AMNH, Hoff slide S–3365); *Nuevo León*: 1 female, Sierra de Enmedio, Hogales Ranch, 26°20′N, 100°40′W, Sept. 1951 (AMNH, Hoff slide S-1971); *San Luis Potosí*: 1 male, km 199, Highway 70, (21°52′N, 99°49′W), 22 February 1973, W. Graham (FSCA, WM3391.01001); *Tamaulipas*: 1 female, Gomez Farias, (23°03′N, 99°09′W), 1 June 1964, Reddell, McKenzie, Mahire (FSCA, WM1834.01001).

Diagnosis.—This small species [e.g. chela (with pedicel) 0.814–0.880 (male), 0.922–1.139 (female) mm in length] has strongly retrorse teeth on the fixed chelal finger, which are only slightly longer than high.

Description.—*Adult:* Color: pedipalps, carapace and coxal region red-brown; abdomen pale red-brown; chelicerae and legs light yellow-brown.

Setae: generally long, straight and acicular.

Chelicera: hand with 5 or 6 setae; movable finger with 1 subdistal seta; galea very slender and elongate; fixed finger with 4 (male, female) small teeth; movable finger with 4 (male, female) teeth; rallum of 4 blades, distal pair with several serrations, basal pair smooth; lamina exterior absent.

Pedipalp (Fig. 16B): trochanter with scattered granulations on most faces, femur granulate on prolateral and basal region of retrolateral margins, patella granulate on prolateral margin, ehelal hand very sparsely granulate on prolateral margin at base of fingers; trochanter 2.27 (male), 2.31 (female), femur 3.20–3.88 (male), 3.50–4.22 (female), patella 2.59–2.75 (male), 2.68–3.14 (female), chela (with pedicel) 3.34–3.64 (male), 3.29–3.60 (female), chela (without pedicel) 3.14–3.43 (male), 3.09–3.43 (female), hand (without pedicel) 1.27–1.53 (male), 1.37–1.58 (female) x longer than broad, movable finger 1.22–1.41 (male), 1.17–1.34 (female) x longer than hand (without pedicel). Fixed chelal finger usually with 22 trichobothria (one female with 20 and 21 trichobothria, one male with 21 trichobothria on both chelae), movable ehelal finger with 10 trichobothria (Fig. 16C): *eb*, *esb* and *isb* in straight row at base of finger; *eb*, *esb*, *isb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 5 trichobothria; *ist* region with 5 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus near *est* region in fixed finger and basal to *t* region in movable finger. Chelal hand with retrolateral condyle small and rounded. Chelal teeth evenly spaced and juxtadentate: fixed finger with 29–36 (male), 30–39 (female) distinct, strongly retrorse teeth; movable finger with ca. 2–3 (male), 3–8 (female) low teeth, plus many additional smaller swellings; base of fixed chelal finger with several small denticles.

Carapace (Fig. 16A): lateral margins evenly convex; with 2 small bulging eyes; anterior margin medially prominent; with 18–23 (male), 19–24 (female) setae including 4 setae on anterior margin and 4 on posterior margin; with very faint posterior furrow situated close to posterior margin.

Coxal region: manducatory process somewhat pointed, with 2 long apical acuminate setae; chaetotaxy 2 + 6: 4: 6: 5: 6 (male); 2 + 5: 4: 5: 4: 4 (female).

Legs: femur + patella 2.23 (male), 2.47 (female) x longer than deep; subterminal tarsal setae trifurcate (Fig. 16E); arolium longer than claws, deeply divided (Fig. 16E).

Abdomen: tergites not divided, medial sternites without medial suture line; sclerites uniseriate. Tergal chaetotaxy: holotype male, 4: 4: 6: 8: 8: 8: 8: 8: 8: 7 (including 4 tactile setae): 8 (including 4 tactile setae): 2; female, 4: 4: 4: 7: 8: 8: 8: 8: 8: 5 (including 3 tactile setae): 6 (including 4 tactile setae): 2. Sternal chaetotaxy: male, 6: (1) 12 [4 + 3] (1): (1) 6 (1): 8: 8: 9: 8: 9: 10: 8 (including 4 tactile setae): 2; female, 7: (1) 6 (1): (1) 6 (1): 8: 7: 8: 8: 9: 10: 8 (including 4 tactile setae): 2; setae of anterior genital operculum (sternite II) of female very small. Setae of tergites and sternites IX–XI acuminate; with several tactile setae.

Genitalia: male with small dorsal apodeme; median genital sac bipartite; female with large gonosac which is covered with scattered pores.

Dimensions (mm): Males: holotype followed by other males (where applicable): Body length 1.85. Pedipalp: trochanter 0.256/0.113, femur 0.515/0.148 (0.474–0.520/0.134–0.148), patella 0.389/0.148 (0.365–0.396/0.139–0.147), chela (with pedicel) 0.884/0.265 (0.814–0.880/0.230–0.258), chela (without pedicel) 0.832 (0.758–0.832), hand (without pedicel) length 0.371 (0.320–0.360), movable finger length 0.477 (0.422–0.462). Chelicera 0.238/? (poorly oriented). Carapace 0.515/0.443; eye diameter 0.030. Leg I: femur 0.256/0.075, patella 0.134/0.077, tibia 0.187/0.056, metatarsus 0.107/0.045, tarsus 0.187/0.035. Leg IV: femur + patella 0.432/0.194, tibia 0.301/0.090, metatarsus 0.164/0.064, tarsus 0.237/0.042.

Females: paratype (WM1244.01001) followed by other females (where applicable): Body length 2.22. Pedipalp: trochanter 0.282/0.122, femur 0.556/159 (0.525–0.688/0.148–0.163), patella 0.429/0.160 (0.390–0.506/0.141–0.161), chela (with pedicel) 0.988/0.300 (0.922–1.139/0.269–0.316), chela (without pedicel) 0.928 (0.856–1.083), hand (without pedicel) length 0.426 (0.394–0.498), movable finger length 0.499 (0.461–0.596). Chelieera 0.281/? (poorly oriented). Carapace 0.563/? (poorly oriented); eye diameter 0.036. Leg I: femur 0.279/0.086, patella 0.147/0.082, tibia 0.220/0.061, metatarsus 0.128/0.048, tarsus 0.198/0.038. Leg IV: femur + patella 0.484/0.196, tibia 0.333/0.090, metatarsus 0.183/0.064, tarsus 0.246/0.045.

Trichobothrial variation.—The female from Tamaulipas (FSCA, WM1834.01001) has a total of 20 trichobothria on the left chela and 21 on the right, and one of the males from 1 mile SW. of Rio Blanco (FSCA, WM1244.01006) has 21 trichobothria on each chela. In each case, the missing trichobothria are absent from the *ist* region.

Remarks.—*Albiorix minor* occurs throughout the Sierra Madre Oriental of eastern Mexico (Fig. 3B).

Etymology.—This species is named for its small size (*minor*, Latin, less).

Albiorix mirabilis Muchmore 1982
Figs. 3C, 17

Albiorix mirabilis Muchmore 1982b: 75–77, figs 33–36; Mahnert 1984a:676, Fig. 46; Harvey 1991:317; Ceballos 2004:428; Harvey et al. 2007:Fig. 5; Harvey 2013:unpaginated.

Material examined.—*Holotype.* **Mexico:** *Oaxaca*: Male, la Cueva de las Maravillas, 6 km S. of Acatlán (de Perez Figueroa) (18°29′N, 96°36′W), 29 December 1976, J.R. Reddell, A. Grubbs, C. Soileau, D. McKenzie (FSCA, WM4675.03001).

Diagnosis.—*Albiorix mirabilis* differs from all other species of the genus by the shape of the teeth on the fixed chelal finger, which are pointed and widely spaced.

Description.—*Adult:* Color: Pale yellow-brown, pedipalps and carapace red-brown.

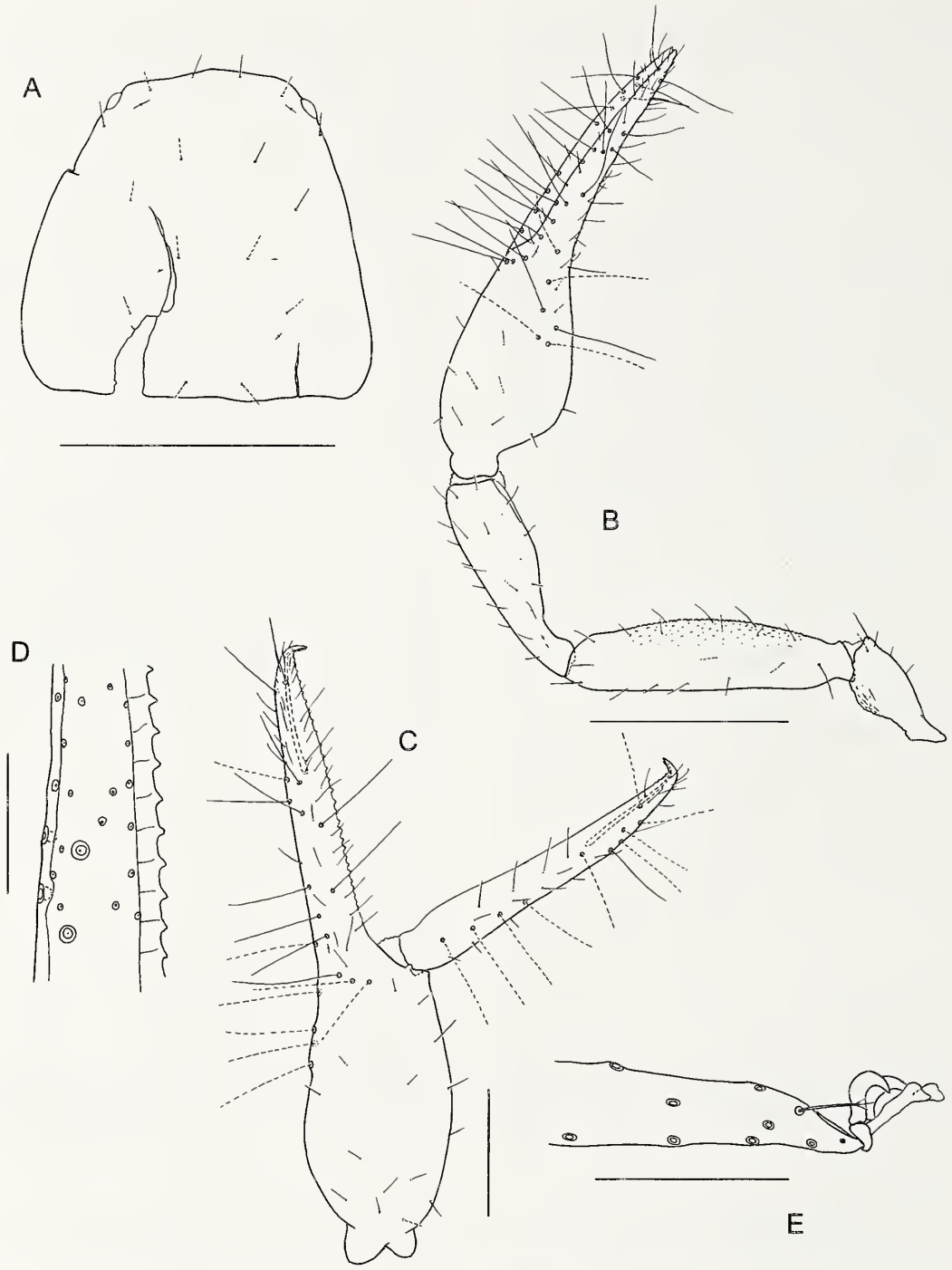

Figure 17.—*Albiorix mirabilis* Harvey & Muchmore sp. nov., male holotype: A. Carapace (flattened during slide preparation); B. Left pedipalp, dorsal; C. Right chela, lateral; D. Detail of fixed chelal finger; E. Tip of left tarsus IV, only subterminal tarsal seta shown. Scale lines = 0.5 mm (A, B); 0.25 mm (C); 0.1 mm (D, E).

Setae: generally long, straight and acicular.

Chelicera: hand with 6 setae; movable finger with 1 subdistal seta; galea very slender and elongate; fixed finger with 5 small teeth; movable finger with 4 teeth; rallum of 4 blades, each with several serrations on anterior margin; lamina exterior absent.

Pedipalp (Fig. 17B): trochanter with scattered granulations, femur and patella lightly granulate on prolateral margin, chelal hand smooth; trochanter 2.32 (male), 4.17 (male), patella 3.39 (male), chela (with pedicel) 3.90 (male), chela (without pedicel) 3.73 (male), hand (without pedicel) 1.59 (male) x longer than broad, movable finger 1.35 (male) x longer than hand (without pedicel). Fixed chelal finger and hand with 22 trichobothria, movable chelal finger with 10 trichobothria (Fig. 17C): *eb*, *esb* and *isb* in straight row at base of finger; *eb*, *esb*, *isb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 5 trichobothria; *ist* region with 6 trichobothria; *est* region with 6 trichobothria; *et* slightly

distal to *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus near *est* region in fixed finger and basal portion of *t* region in movable finger. Chelal hand with retrolateral condyle small and rounded. Chelal teeth evenly spaced and juxtadentate: fixed finger with ca. 32 small pointed teeth; movable finger with 4 very low teeth at distal end, the remainder absent; base of fixed chelal finger with several small denticles.

Carapace (Fig. 17A): lateral margins evenly convex; with 2 small bulging eyes; anterior margin medially prominent; with 16 setae including 4 setae on anterior margin and 2 on posterior margin; with 1 posterior furrow.

Coxal region: manducatory process somewhat pointed, with 2 long apical acuminate setae; chaetotaxy 2 + 6: 5: 5: 4–5: 6 (♂).

Legs: femur + patella 2.54 (male) x longer than deep; subterminal tarsal setae with trifurcate, each tine quite long (Fig. 17E); arolium longer than claws, deeply divided (Fig. 17E).

Abdomen: tergites not divided, medial sternites without medial suture line; sclerites uniseriate. Tergal chaetotaxy: male, 4: 4: 6: 6: 8: 8: 8: 8: 8: 8 (including 4 tactile setae): 7 (including 4 tactile setae): 2. Sternal chaetotaxy: male, 11: (1) 8 [3 + 3] (1): (1) 6 (1): 9: 9: 9: 10: 10: 10: 8 (including 4 tactile setae): 2. Setae of tergites and sternites IX–XI acuminate; with several tactile setae.

Genitalia: male with medium-sized dorsal apodeme; median genital sac apparently bifurcate.

Dimensions (mm): Male holotype: Body length 2.10. Pedipalp: trochanter 0.327/0.141, femur 0.722/0.173, patella 0.566/0.167, chela (with pedicel) 1.216/.312, chela (without pedicel) 1.163, hand (without pedicel) length 0.496, movable finger length 0.670. Chelicera 0.290/0.131. Carapace 0.660/0.646 (flattened); eye diameter 0.045. Leg I: femur 0.353/0.093, patella 0.175/0.093, tibia 0.256/0.064, metatarsus 0.165/0.052, tarsus 0.250/0.038. Leg IV: femur + patella 0.571/0.225, tibia 0.410/0.101, metatarsus 0.221/0.070, tarsus 0.307/0.045.

Remarks.—*Albiorix mirabilis* has only been found in Cueva de las Maravillas, which is situated near the town of Acatlán de Perez Figueroa, in southern Mexico (Fig. 3C). The original description by Muchmore (1982b) is quite detailed, but we here provide a new description and new figures of the only known specimen, the male holotype.

Albiorix oaxaca Harvey & Muchmore, sp. nov.
Figs. 3C, 18

Material examined.—*Holotype.* MEXICO: *Oaxaca*: male, Huatla de Jiménez (18°08′N, 96°51′W), 9 November 1968, Reyes and Cabrera (FSCA, WM7260.01001).

Diagnosis.—This is one of the largest species of the genus, and is approached in size only by *A. anophthalmus*, *A. chilensis*, *A. magnus* and *A. meraculus*. It is easily distinguished by the morphology of the subterminal tarsal seta which has 1 very long distal tine and 2 short basal tines (Fig. 18E).

Description.—*Adult:* Color: pedipalps, carapace and coxal region deep red-brown; abdomen red-brown; chelicerae and legs light yellow-brown.

Setae: generally long, straight and acicular.

Chelicera: hand with 6 setae; movable finger with 1 subdistal seta; galea very slender and elongate, slightly curved; fixed finger with 6 teeth as well as 2 small teeth; movable finger with 7 teeth; rallum of 4 blades, each with several serrations; lamina exterior absent.

Pedipalp (Fig. 18B): trochanter lightly granulate on retrolateral face, femur lightly granulate over most surfaces but with stronger granulations on prolateral face, patella lightly granulate over prolateral face, chela with light granulations on prolateral face but otherwise fairly smooth; trochanter 2.29 (male), femur 4.12 (male), patella 3.21 (male), chela (with pedicel) 3.69 (male), chela (without pedicel) 3.47 (male), hand (without pedicel) 1.57 (male) x longer than broad, movable finger 1.29 (male) x longer than hand (without pedicel). Fixed chelal finger and hand with 22 trichobothria, movable chelal finger with 10 trichobothria (Figs. 3C, 18C): *eb*, *esb* and *isb* in straight row at base of finger; *eb*, *esb*, *isb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 5 trichobothria; *ist* region with 6 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus at anterior end of *est* region in fixed finger and basal to the *t* region in movable finger. Chelal hand with retrolateral condyle small and rounded. Chelal teeth evenly spaced and juxtadentate: fixed finger with 70 retrorse, close-set teeth (Fig. 18D); movable finger with several distal teeth none of which are upraised, leading into many very low teeth which extend along entire length of finger; base of fixed chelal finger with several small denticles.

Carapace (Fig. 18A): lateral margins evenly convex; 0.96 (male) x longer than broad; with 2 small bulging eyes; anterior margin medially prominent; with 23 setae including 4 setae on anterior margin and 4 on posterior margin; without furrows.

Coxal region: manducatory process somewhat pointed, with 2 long apical acuminate setae; chaetotaxy 2 + 7: 5: 6: 6: 7.

Legs: femur + patella 2.88 (male) x longer than deep; metatarsus and tarsus III and IV with sub-basal tactile seta; subterminal tarsal setae with 1 very long distal tine and 2 short basal tines (Fig. 18E); arolium longer than claws, deeply divided.

Abdomen: tergites and sternites not divided; sclerites uniseriate, except for sternite II, which has 2 irregular rows and sternite III, which has 1 seta placed slightly in advance of others. Tergal chaetotaxy: male: 4: 5: 8: 9: 8: 9: 10: 9: 9: 9 (including 2 lateral tactile setae): 8 (including 4 tactile setae): 2. Sternal chaetotaxy: male: 10: (1) 15 [3 + 3] (1): (1) 7 (1): 14: 10: 11: 11: 10: 11: 8 (including 4 tactile setae): 2. Setae of tergites and sternites IX–XI acuminate.

Genitalia: male with small dorsal apodeme; median genital sac not preserved in specimen.

Dimensions (mm): Male: holotype: Body length 2.96. Pedipalp: trochanter 0.48/0.21, femur 1.03/0.25, patella 0.835/0.26, chela (with pedicel) 1.81/0.49, chela (without pedicel) 1.70, hand (without pedicel) length 0.77, movable finger length 0.99. Chelicera 0.445/0.21, movable finger length 0.275. Carapace 0.85/0.89 (but distorted on slide); eye diameter 0.045. Leg I: femur 0.494/0.134, patella 0.268/0.125, tibia 0.396/0.091, metatarsus 0.205/0.072, tarsus 0.314/0.058.

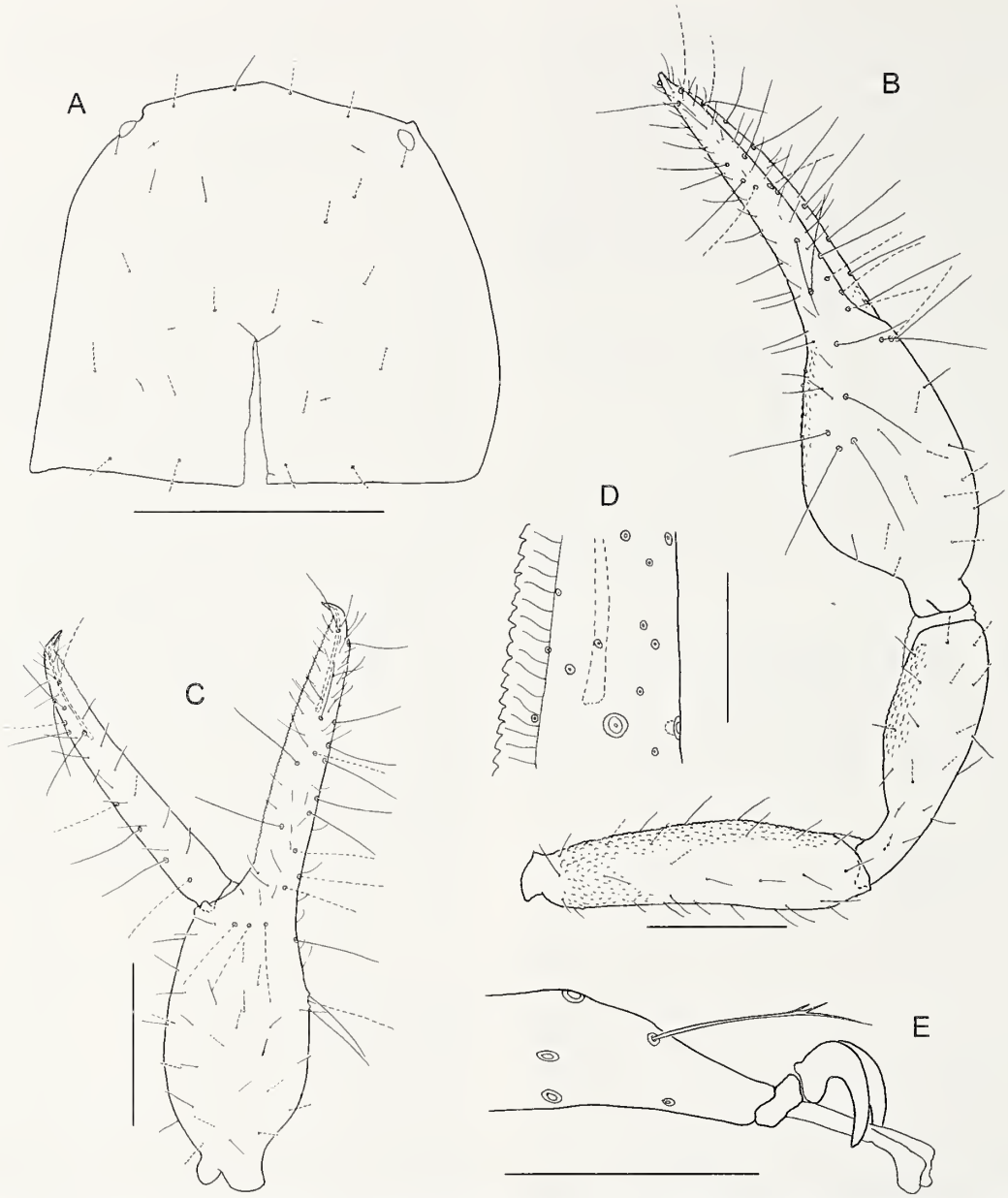

Figure 18.—*Albiorix oaxaca* Harvey & Muchmore sp. nov., male holotype: A. Carapace (flattened during slide preparation); B. Right pedipalp, dorsal (without trochanter); C. Left chela, lateral; D. Detail of fixed chelal finger; E. Tip of left tarsus IV, only subterminal tarsal seta shown. Scale lines = 0.5 mm (A, B); 0.2 mm (C); 0.1 mm (D, E).

Leg IV: femur + patella 0.865/0.30, tibia 0.58/0.14, metatarsus 0.30/0.105, tarsus 0.45/0.065.

Remarks.—*Albiorix oaxaca* has only been found in the state of Oaxaca in southern Mexico (Fig. 3C).

Etymology.—The specific epithet is a noun in apposition taken from the type locality.

Albiorix parvidentatus Chamberlin 1930
Figs. 1A, 1B, 3A, 6B–F, 7E–H, 19

Albiorix parvidentatus Chamberlin 1930:45–46; Beier 1932a:173; Roewer 1936:Fig. 30b; Roewer 1937:257; Hoff 1958:15; Harvey 1991:318; Harvey 2013:unpaginated.

Material examined.—*Holotype*. USA: *California:* male, Palm Canyon, Riverside County (33°48′N, 116°31′W), 5 April 1925, under stone, J.C. Chamberlin (CAS, Entomology Type No. 17458, JC–535.02001).

Other material. MEXICO: *Baja California*: 1 female, El Mayor (32°08′N, 115°16′W), 4 April 1939, no collector (UCDC). USA: *Arizona*: 1 female, Cochise County, 3 miles E. of Portal (31°55′N, 109°04′W), 11 September 1950, W.J. Gertsch (AMNH, Hoff slide S–1586.1); 1 female, Cochise County, Cave Creek Canyon, South-West Research Station (31°52′N, 109°13′W), 22 August 1956, A.F. Archer (AMNH, Hoff slide S–3518); 2 females, Cochise County, Chiricahua Mountains (31°56′N, 109°23′W), 5,400 feet, 14 April 1961, P. Wygodzinsky (UCDC); 15 males, 12 females, Cochise County, Chiricahua Mountains, 3 miles N. of Portal (31°57′N, 109°08′W), 23 March 1984, under rocks, W. and E. MacKay (FSCA, WM6559); 1 male, Cochise County, Huachuca

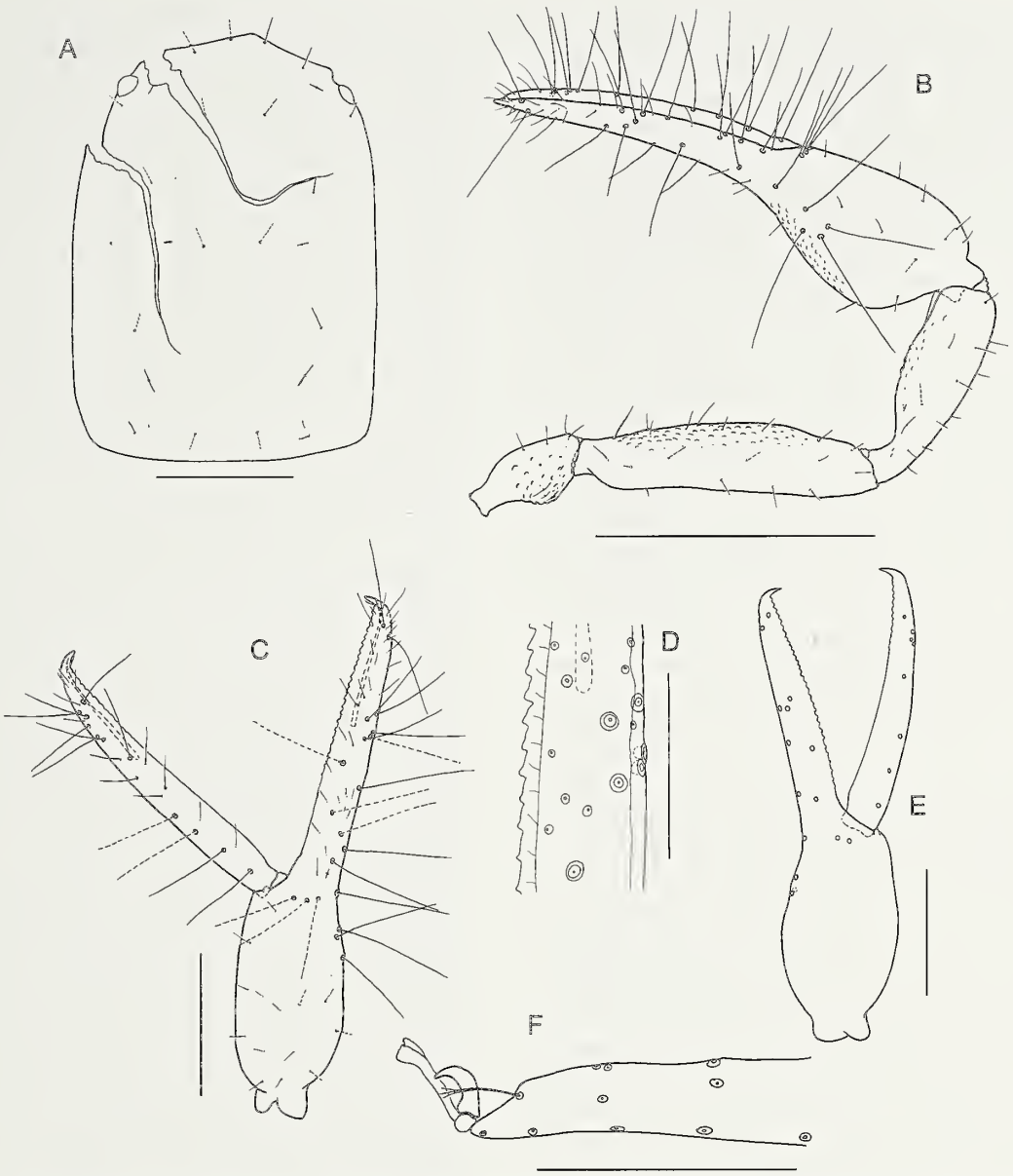

Figure 19.—*Albiorix parvidentatus* Chamberlin, male holotype, unless stated otherwise: A. Carapace, dorsal; B. Right pedipalp, dorsal; C. Left chela, lateral; D. Detail of fixed chelal finger; E. Right chela, lateral, tritonymph (CAS, JC–547.01003); F. Tip of right tarsus IV, only subterminal tarsal seta shown. Scale lines = 0.5 mm (B, C, E); 0.2 mm (A); 0.1 mm (D, F).

Mountains (31°24′N, 110°18′W), 2009, J. Cowles (WAM T108162); 2 males, Cochise County, Upper Carr Canyon, Huachuca Mountains (31°26′N, 110°18′W), 22 July 1955, W.J. Gertsch (AMNH, Hoff slide S–3406.1–2); 1 female, Gila County, 2 miles S. of Payson (34°13′N, 111°19′W), 11 April 1935, W. Ivie (CAS, JC–1360.01001); 2 males, 2 females, Gila County, 8 miles N. of [Theodore] Roosevelt Dam (33°40′N, 111°10′W), 11 April 1935, W. Ivie (CAS, JC–1371.01001–4); 2 females, Graham County, Marijilda (as Naritilda) Canyon, Graham Mountains (32°42′N, 109°47′W), 5,100 feet, 7 April 1961, P. Wygodzinsky (UCDC); 2 females, Graham County, Noon Creek, Graham Mountains (32°40′N, 109°47′W), 7 April 1961, P. Wygodzinsky (UCDC); 1 male, Maricopa County, junction of Mesa and Salt Rivers (33°27′N, 111°51′W), 9 April 1935, W. Ivie (CAS, JC–1372.04001); 1 female, Maricopa County, Seven Springs (33°58′N, 111°51′W), August 1966 (MCZ, WM1628.01001); 1 female, Pima County, Arkenstone Cave, Colossal Cave Mountain Park, at gate (entrance) to cave (32°04′N, 110°38′W), 29 July 1990, R.B. Pape (FSCA, WM7539.01001); 1 ♂, 3 ♀, Pima County, Arkenstone Cave, Colossal Cave Mountain Park, at gate (entrance) to cave (32°04′N, 110°38′W), 21 March 1998, R.B. Pape (FSCA, WM8234); 1 male, Pima County, Baboquivari Mountains, Brown Canyon (31°45′N, 111°31′W), 19 July 1959, V. Roth (AMNH, WM1736.02001); 1 male, Pima County, Baboquivari Canyon, west side, Baboquivari Mountains (31°47′N, 111°37′W), 25–27 August 1952, H.B. Leech, J.W. Green (UCDC); 2 males, Pima County, Elkhorn Ranch, E. slope of N. end Baboquivari Mountains (31°49′N, 111°32′W), 28 July 1952, H.B. Leech, J.W. Green (UCDC); 1 female, Pima County, Gates Pass, near Tucson (32°13′N, 111°06′W), 28 March 2009, J. Cowles (WAM T108158); 1 male, 1 female, Pima County, Sabino

Basin, Santa Catalinas (32°20′N, 110°48′W), 8–12 July 1916 (AMNH, Hoff slide S–185.1–2); 1 male, Pima County, Santa Catalina Mountains (32°25′N, 110°42′W), 25 May 1936, Bryant (AMNH, Hoff slide S–194.1); 1 female, Pima County, Tucson (32°13′N, 110°56′W), 1 April 1936, Bryant (AMNH, Hoff slide S–189); 1 female, Pima County, Tucson Mountains (32°13′N, 111°07′W), 15 February 1957, V. Roth (AMNH, Hoff slide S–3520); 12 males, 11 females, 1 tritonymph, Pima County, Tucson, 12740 East Chukut Trail (32°17′23″N, 110°43′13″W), 21 January 2013, under rock on hillside, M.S. Harvey, F. Harvey (WAM T129246, T129656); 1 male, Pima County, Vail (32°00′N, 110°42′W), 2 July 2009, J. Cowles (WAM T108161); 1 male, 1 female, Pinal County, Oracle (32°37′N, 110°46′W), 7 March 1980, decaying sotol clump (*Dasylirion wheeleri*), D.W. Zeh (FSCA, WM5979.01001–2); 1 female, Santa Cruz County, 5 miles NE. of Patagonia (31°35′N, 110°42′W), 14 September 1991, R.B. Pape (FSCA, WM8093); 1 tritonymph, Yuma County, Fortuna Mine (32°33′N, 114°20′W), 27 January 1957, V. Roth (AMNH, Hoff slide S–4102); 1 male, 1 female, Yuma County, Fortuna Mine (32°33′N, 114°20′W), 7 February 1960, V. Roth (AMNH, Hoff slide S–4103.1–2); 1 male, 1 female, Yuma County, 2 miles W. of Ligurta (32°40′N, 114°18′W), 15 January 1983, G. Lowe (WAM T127031); 2 males, 1 female, Yuma County, Palm Canyon (33°22′N, 114°06′W), 18 November 1961, D. Tuttle (UCDC); 1 male, Yuma County, Palm Canyon (33°22′N, 114°06′W), 10 May 1958, V. Roth (AMNH, Hoff slide S–4089); 1 male, Yuma County, Palm Canyon, Kofa Mountains (33°22′N, 114°06′W), 10 March 1960, V. Roth (AMNH, Hoff slide S–4094); 2 males, 1 female, Yuma County, canyon north of Palm Canyon (33°22′N, 114°06′W), 6 March 1960, V. Roth (AMNH, Hoff slide S–4096.1–3); *California*: 1 female, Imperial County, El Centro (32°48′N, 115°34′), 8 December 1927, F.R. Blaisdell (CAS, JC–375.02001); 1 female, Imperial County, Julian Wash, Black Mountain Road (33°05′N, 114°42′W), 15 January 1983, G. Lowe (WAM T127034); 2 females, Inyo County, Beveridge Canyon, Inyo Mountains (36°43′N, 117°51′W), 6,500 feet, 4 June 1975, D. Giuliani (FSCA, WM4905.02001–2); 1 male, 1 female, Inyo County, White Mountains, 6.4 miles NE. of Big Pine (37°14′N, 118°13′W), 25 April –22 July 1982, ethylene glycol can trap, D. Giuliani (FSCA, WM7704); 2 males, 1 female, Los Angeles County, Mt Baldy Rd, below Mt Baldy village (34°14′N, 117°40′W), 15 April 1987, under rock, G. Lowe (WAM T127033); 1 female, Los Angeles County, San Clemente Island (32°54′N, 118°30′W), 10 April 1923, Crosby (CAS, JC–734.02001); 1 male, Los Angeles County, Switzers Camp, Angeles Forest Highway (34°15′31″N, 118°09′18″W), 27 June 1985, G. Lowe (WAM T127036); 1 tritonymph, Orange County, Laguna Beach [33°32′N, 117°46′W], 28 December 1932, W. Ivie (CAS, JC–1748.02001); 1 male, 1 female, Orange County, Laguna Beach (33°32′N, 117°46′W), 22 July 1931, W. Ivie (CAS, JC–1628.01001–2); 1 male, Orange County, Santa Ana, Irvine Park (33°45′N, 117°56′W), 17 July 1931, W. Ivie (CAS, JC–1824.01001); 3 males, Riverside County, 2 miles SE. of Cabazon, base of mountains (33°53′N, 116°46′W), 9 April 1982, G. Lowe (WAM T127035); 1 male, Riverside County, Coyote Canyon (33°40′N, 116°22′W), 12 December 1963, ex fern, W.H. Ewart (UCRC, WM4278; Univ. California Insect Survey Specimen # 306795); 1 female, Riverside County, Deep Canyon, 1/2 mile S. of Pinyon Crest (turn off), Santa Rosa Mountains (33°41′N, 116°22′W), 3,600 feet, 5 April 1974, under rock, W. Icenogle (UCRC, WM5380); 5 males, 2 females, Riverside County, Deep Canyon, 1/2 mile S. of Pinyon Crest (turn off), Santa Rosa Mountains (33°41′N, 116°22′W), 3,600 feet, 16 April 1974, under rocks in ravine, W. Icenogle (UCRC, WM5381); 1 male, Riverside County, Lake Herender [not traced], 14 April 1956, from desert plants, I.M. Newell (AMNH, Hoff slide S–3533); 18 males, 6 females, 1 tritonymph, Riverside County, Lamb Canyon, 2 miles NW. of Gilman Hot Springs (33°51′N, 117°01′W), 1,520 feet, 4 March 1979–23 December 1980, coastal sage scrub, hillside, ethylene glycol can trap, R.L. Aalbu (FSCA, WM6300); 2 tritonymph exuviae, Riverside County, near Riverside (33°57′N, 117°24′W), 26 November 1925, under stone on a desert hillside, J.C. Chamberlin (CAS, JC–547.01003); 1 male, Riverside County, Santa Rosa Mountains, Deep Canyon (33°41′N, 116°22′W), 27 April 1979, W. Icenogle (UCRC, WM6050.01001); 1 female, Riverside County, Snow Creek (33°53′29″N, 116°41′27″W), 29 June 2002, under rock, M.S. Harvey (WAM T127032); 2 males, San Diego County, Anza Borrego State Park,Box Canyon (33°15′N, 116°24′W), 14 April 1981, D. Ubick (CAS); 1 male, San Diego County, Anza-Borrego Desert State Park (33°14′N, 116°16′W), 26 March 1991, D. Ubick (CAS); 1 male, San Diego County, Sheep Canyon, Borrego State Park (33°20′N, 116°29′W), 27 April 1955, R.O. Schuster (UCDC, Hoff slide S–3360.1); 1 male, Tulare County, Lindsay (36°12′N, 119°05′W), 13 March 1963, W.H. Ewart (UCRC, WM4276); *New Mexico*: 2 males, Catron County, Deep Creek, 13 miles NE. of Glenwood (33°27′N, 108°46′W), 30 July 1979, A. Grubbs (FSCA, WM5855.01001–2).

Diagnosis.—The combined presence of eyes (Fig. 19A), prolateral face of the chelal hand granulate (Fig. 19B), trifurcate subterminal tarsal setae with short tines of equal length (Fig. 19F), median teeth of the fixed chelal finger noticeably longer than high and with a noticeably sinuate distal face (Fig. 19D), 22 trichobothria on the fixed chelal finger and hand (Figs. 5L, 19C), and trichobothrium ib_5 situated on approximately same level as *eb*, *esb* and *isb*, and est_4 situated within the *ist* region (Figs. 19C) distinguishes *A. parvidentatus* from all species of the genus.

Description.—*Adult:* Color: pedipalps, carapace and coxal region red-brown; abdomen pale red-brown; chelicera and legs light yellow-brown.

Setae: generally long, straight and acicular.

Chelicera: hand with 6, or very rarely 5 or 7 setae; movable finger with 1 subdistal seta; galea very slender and elongate; fixed finger with 2 (male), 6 (female) small teeth; movable finger with 2 (male), 6 (female) teeth; rallum of 4 blades, each with several serrations; lamina exterior absent.

Pedipalp (Fig. 19B): trochanter with scattered granulations, femur granulate on most faces, but coarsely granulate on prolateral surface, patella lightly granulate on prolateral margin, chelal hand lightly granulate on prolateral surface at base of fingers; trochanter 2.06–2.56 (male), 2.17–2.48 (female), femur 3.69–4.48 (male), 3.62–4.65 (female), patella 2.71–3.42 (male), 2.61–3.34 (female), chela (with pedicel) 3.30–4.31 (male), 3.17–4.14 (female), chela (without pedicel) 3.09–4.06 (male), 2.96–3.93 (female), hand (without pedicel) 1.20–1.63 (male), 1.28–1.58 (female) x longer than broad, movable finger 1.28–1.69 (male), 1.24–1.62 (female) x longer than hand (without pedicel). Fixed chelal finger and hand with 22

trichobothria, movable chelal finger with 10 trichobothria (Fig. 19C): *eb*, *esb* and *isb* in straight row at base of finger; *eb*, *esb*, *isb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 5 trichobothria; *ist* region with 6 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus within *est* region in fixed finger and basal to *t* region in movable finger. Chelal hand with retrolateral condyle small and rounded. Chelal teeth evenly spaced and juxtadentate: fixed finger with 29–53 (male), 31–49 (female) low, retrorse teeth; movable finger with ca. 3–15 (male), 5–12 (female) very low teeth, followed by undulations; base of fixed chelal finger with several small denticles.

Carapace (Fig. 16A): lateral margins evenly convex; with 2 small bulging eyes; anterior margin medially prominent; with 18–22 (male), 17–21 (female) setae including 4 setae on anterior margin and 4 (rarely 5) on posterior margin; with very faint posterior furrow situated close to posterior margin.

Coxal region: manducatory process somewhat pointed, with 2 long apical acuminate setae; ehaetotaxy 2 + 5–7: 4: 5: 5: 4 (holotype male); 2 + 7: 5: 5: 5: 6 (female).

Legs: femur + patella 2.14–2.71 (male), 2.30–2.92 (female) x longer than deep; subterminal tarsal setae trifurcate (Fig. 16E); arolium longer than claws, deeply divided (Fig. 16E).

Abdomen: tergites and sternites not divided; sclerites uniseriate, except for sternite II and III of males, which have scattered setae. Tergal chaetotaxy: holotype male, 2: 4: 4: 6: 7: 6: 6: 6: 6: 6 (including 2 tactile setae): 8 (including 4 tactile setae): 2; female, 4: 4: 5: 8: 8: 8: 8: 7: 6: 7: 7 (including 4 tactile setae): 2. Sternal chaetotaxy: male holotype, 7: (1) 6 [3 + 3] (1): (1) 6 (1): 8: 9: 8: 8: 8: 6: 8 (including 4 tactile setae): 2; female from Snow Creek, 10: (1) 5 (1): (1) 6 (1): 9: 9: 8: 9: 11: 8: 10 (including 4 tactile setae): 2; setae of anterior genital operculum (sternite II) of female very small. Setae of tergites and sternites IX–XI acuminate; with several tactile setae.

Genitalia: male with small dorsal apodeme; median genital sac deeply bipartite; female with large gonosac, which is covered with scattered pores.

Dimensions (mm): Males: holotype followed by other males (where applicable): Body length 1.76 (1.70–3.15). Pedipalp: trochanter 0.224/0.109 (0.243–0.385/0.109–0.154), femur 0.550/0.124 (0.513–0.844/0.128–0.205), patella 0.397/0.128 (0.386–0.640/0.132–0.187), chela (with pedicel) 0.941/0.240 (0.872–1.400/0.252–0.396), chela (without pedicel) 0.896 (0.82–1.328), hand (without pedicel) length 0.334 (0.333–0.557), movable finger length 0.557 (0.493–0.824). Chelicera 0.216/0.097, movable finger length 0.122. Carapace 0.544/0.400 (0.479–0.665/0.432–0.550); eye diameter 0.031. Leg I: femur 0.275/0.069, patella 0.139/0.068, tibia 0.202/0.048, metatarsus 0.125/0.041, tarsus 0.195/0.032. Leg IV: femur + patella 0.461/0.204 (0.421–0.659/0.185–0.293), tibia 0.306/0.077, metatarsus 0.164/0.058, tarsus 0.261/0.032.

Females: specimen from Snow Creek, California (WAM T127032) followed by other females (where applicable): Body length 2.64 (2.03–3.05). Pedipalp: trochanter 0.382/0.161 (0.295–0.422/0.123–0.172), femur 0.739/0.191 (0.582–0.957/0.141–0.224), patella 0.600/0.205 (0.432–0.688/0.147–0.247), chela (with pedicel) 1.424/0.383 (1.106–1.514/0.272–0.444), chela (without pedicel) 1.352 (0.958–1.427), hand (without pedicel) length 0.560 (0.400–0.610), movable finger length 0.816 (0.531–0.848). Chelicera 0.319/0.145, movable finger length 0.187. Carapace 0.720/0.510 (0.547–0.780/0.429–0.630); eye diameter 0.045. Leg I: femur 0.390/0.098, patella 0.203/0.090, tibia 0.328/0.062, metatarsus 0.180/0.050, tarsus 0.252/0.037. Leg IV: femur + patella 0.610/0.232 (0.471–0.659/0.179–0.247), tibia 0.450/0.100, metatarsus 0.230/0.072, tarsus 0.335/0.042.

Tritonymph: Chelicera: galea long, slightly curved; hand with 6 setae, movable finger with 1 seta; rallum composed of 4 blades, all serrate.

Pedipalp: trochanter 1.73, femur 2.72, patella 2.72, chela (with pedicel) 4.49, chela (without pedicel) 4.24 × longer than broad. Fixed finger with 15 trichobothria, movable finger with 8 trichobothria (Fig. 19E); *eb*, *esb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 3 trichobothria; *ist* region with 3 trichobothria; *est* region with 4 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *st* region with 1 trichobothrium; *t* region with 5 trichobothria; *isb* and *sb* absent. Chelal hand with retrolateral condyle small and rounded.

Carapace: anterior margin medially prominent; 1 pair of small eyes present; with 18 setae, including 4 setae on anterior margin and 4 setae on posterior margin.

Coxal region: posterior maxillary lyrifissure present, subbasal.

Legs: much as in adults.

Dimensions (mm): Body length 1.28. Pedipalp: trochanter 0.242/0.147, femur 0.490/0.133, patella 0.364/0.134, chela (with pedicel) 0.854/0.190, chela (without pedicel) 0.806, hand (without pedicel) length 0.317, movable finger length 0.513. Carapace 0.435/0.390.

Trichobothrial variation.—The four specimens from Los Angeles County, California (WAM T127033, T127036 and CAS JC–734.02001) and one of the males from San Diego County (Anza-Borrego) (CAS) each have only 20 trichobothria on both chelal fingers, which is generally formed by the presence of only 4 trichobothria in the *ib* region and 5 in the *ist* region. In one specimen from Switzer Camp (WAM T127036), there are 4 trichobothria in the *ib* region and only 4 in the *ist* region. The two females from Marijilda Canyon, Arizona (UCDC) appear to have only 21 trichobothria on each chela with a single trichobothrium absent from the *ist* region. The uncertainty is due to the poor quality of the slide preparations. The male from Fortuna Mine, Arizona (AMNH Hoff slide S-4103.1) has only 21 trichobothria on the left chela and 22 trichobothria on the right chela, with the missing trichobothrium from the *ist* region.

Remarks.—Chamberlin (1930) described and named this species from the adult holotype male from Palm Canyon, California. He also had listed a "dead and immature female (JC–547.01003), together with its cast skin." This slide-mounted material actually consists of the exuviae of two tritonymphs, along with a single silken molting chamber, which is included in the slide-mount.

There is considerable size variation within this species but there appear to be no consistent features that may be used to suggest there is more than one species present. For example, the two specimens (the male holotype and a female from Snow Creek) used to provide much of the individual data in the

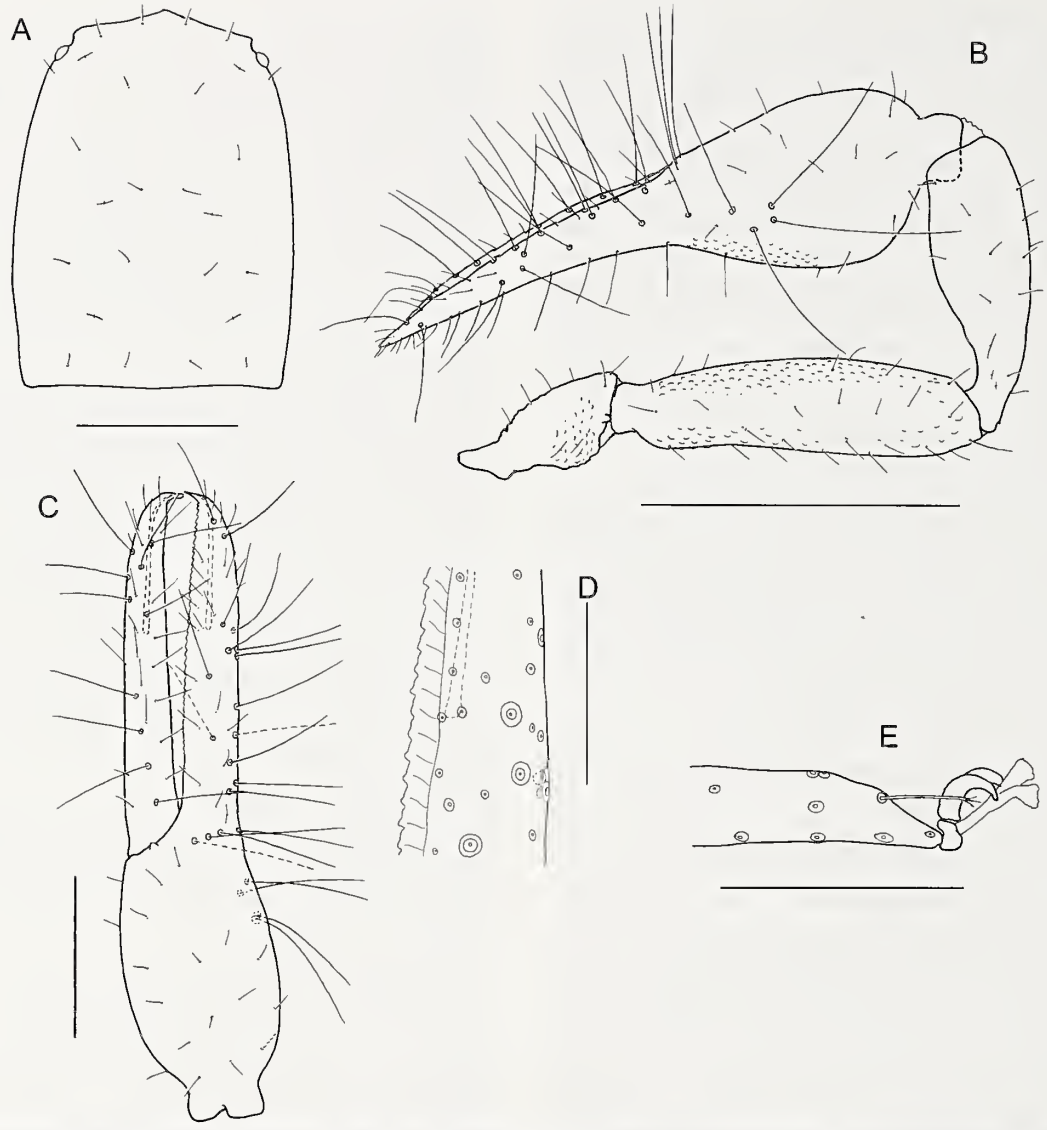

Figure 20.—*Albiorix puebla* Harvey & Muchmore sp. nov., male holotype: A. Carapace, dorsal; B. Right pedipalp, dorsal; C. Left chela, lateral; D. Detail of fixed chelal finger; E. Tip of right tarsus IV, only subterminal tarsal seta shown. Scale lines = 0.5 mm (B); 0.25 mm (A, C); 0.1 mm (D, E).

description were collected only 19 km apart but are considerably different in size, as the male holotype has a chela (with pedicel) length of 0.94 mm and the female from Snow Creek is 1.42 mm.

Albiorix parvidentatus is found throughout southern California, Arizona, south-western New Mexico and north-western Mexico (Fig. 3A). Specimens are most frequently recorded under rocks in dry ecosystems.

Albiorix puebla Harvey & Muchmore, sp. nov.
Figs. 3C, 20

Material examined.—*Holotype*. MEXICO: *Puebla*: male, Tehuacán (18°28′N, 97°24′W), 6 July 1941, H. Dybas (CAS, JC–2190.01001).

Paratype. 1 male, collected with holotype (CAS, JC–2190.01002).

Diagnosis.—*Albiorix puebla* shares with *A. retrodentatus* the strongly sinuate distal face of the teeth of the fixed chelal finger, but is slightly smaller (e.g., chela (with pedicel) length 0.963–0.976 mm versus 1.065–1.448 mm in *A. retrodentatus*), and trichobothrium ist_1 is situated directly dorsal to ist_3, but is slightly dorso-distal to ist_3 in *A. retrodentatus*.

Description.—*Adult:* Color: pedipalps and carapace red-brown, legs and chelieerae light brown.

Setae: generally long, straight and acicular.

Chelicera: hand with 6 setae; movable finger with 1 subdistal seta; galea very slender and elongate; fixed finger with 3 (male) small teeth; movable finger with 3 (male) teeth; rallum of 4 blades, each with several serrations; lamina exterior absent.

Pedipalp (Fig. 20B): trochanter granulate on all faces, femur and patella lightly granulate on prolateral margin, chelal hand with granulations on prolateral margin at base of fingers; trochanter 2.19–2.35 (male), femur 4.01–4.08 (male), patella 2.95–3.05 (male), chela (with pedicel) 3.64–3.76 (male), chela (without pedicel) 3.43–3.56 (male), hand (without pedicel) 1.39–1.48 (male) x longer than broad, movable finger

1.41–1.44 (male) x longer than hand (without pedicel). Fixed chelal finger and hand with 22 trichobothria, movable chelal finger with 10 trichobothria (Fig. 20C): *eb*, *esb* and *isb* in straight row at base of finger; *eb*, *esb*, *isb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 5 trichobothria; *ist* region with 6 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus within *est* region in fixed finger and basal to *t* region in movable finger. Chelal hand with retrolateral condyle small and rounded. Chelal teeth evenly spaced and juxtadentate: fixed finger with 31–36 (♂) low, retrorse teeth, most with strongly sinuate distal face; movable finger with ca. 1–5 (♂) low teeth; base of fixed chelal finger with several small denticles.

Carapace (Fig. 20A): lateral margins evenly convex; with 2 small bulging eyes; anterior margin medially prominent; with 20 setae including 4 setae on anterior margin and 4 on posterior margin; with very faint posterior furrow situated close to posterior margin.

Coxal region: manducatory process somewhat pointed, with 2 long apical acuminate setae; chaetotaxy 2 + 7: 5: 6: 6: 7 (male).

Legs: femur + patella 2.27–2.36 (male) x longer than deep; subterminal tarsal setae trifurcate (Fig. 20E); arolium longer than claws, deeply divided (Fig. 20E).

Abdomen: tergites and sternites not divided; sclerites uniseriate. Tergal chaetotaxy: male, 4: 4: 6: 6: 7: 8: 8: 8: 6: 7 (including 4 tactile setae): 7 (including 4 tactile setae): 2. Sternal chaetotaxy: male, 7: (1) 14 [3 + 3] (1): (1) 8 (1): 10: 11: 11: 11: 9: 9: 8 (including 4 tactile setae): 2. Setae of tergites and sternites IX–XI acuminate; with several tactile setae.

Genitalia: male with small dorsal apodeme; median genital sac deeply bipartite.

Dimensions (mm): Males: holotype followed by paratype (where applicable): Body length ca. 2.0 (ca. 1.8). Pedipalp: trochanter 0.280/0.128 (0.258/0.110), femur 0.595/0.146 (0.589/0.147), patella 0.454/0.149 (0.448/0.152), chela (with pedicel) 0.976/0.268 (0.963/0.256), chela (without pedicel) 0.920 (0.912), hand (without pedicel) length 0.372 (0.378), movable finger length 0.536 (0.534). Chelicera 0.256/0.148. Carapace 0.575/0.433 (0.555/0.403); eye diameter 0.030. Leg I: femur 0.274/0.078, patella 0.137/0.072, tibia 0.224/0.053, metatarsus 0.134/0.042, tarsus 0.211/0.033. Leg IV: femur + patella 0.485/0.214 (0.467/0.198), tibia 0.340/0.084, metatarsus 0.175/0.061, tarsus 0.260/0.040.

Remarks.—*Albiorix puebla* is a small species that is similar to *A. retrodentatus*, but is substantially smaller and has trichobothrium ist_1 in a slightly different position. It is known only from a single location in the southeastern region of Puebla state, in southern Mexico, some 230 km east of *A. retrodentatus* and not far from the only known collection localities of *A. mirabilis* and *A. oaxaca* (Fig. 3C).

Etymology.—The specific epithet is a noun in apposition based on Puebla, the Mexican state in which the type locality is based.

Albiorix retrodentatus Hoff 1945
Figs. 3C, 21

Albiorix retrodentatus Hoff 1945:6–8, figs 10–16; Hoff 1958:15; Hoff 1959:4, etc.; Rowland and Reddell 1976:16; Harvey 1991:318; Ceballos 2004:428; Harvey 2013:unpaginated.

Albiorix bolivari Beier 1963:133–134, Fig. 1. **Syn. nov.**

Not *Albiorix retrodentatus* Hoff: Hoff 1956:25–26 (misidentification; see *Albiorix conodentatus* Hoff).

Material examined.—*Holotype of* A. retrodentatus. MEXICO: *Guerrero*: male, Mexcala (17°56′N, 99°37′W), 2 July 1941, L.I. Davis (AMNH, Hoff slide S–114.5–5453).

Paratype A. retrodentatus. MEXICO: *Guerrero*: 1 male, same data as holotype (AMNH, Hoff slide S–114.3–5202).

Paratypes of A. bolivari. MEXICO: *Guerrero:* 2 male, Gruta de Acuitlapán, 12 km NE. of Taxco (18°35′N, 99°35′W), 1,500 m, 5 May 1963, C. Bolivar *et al.* (CNAN, WM1820.01001–2).

Other material. MEXICO: *Michoacan:* 1 tritonymph, 5 miles SW. of Tiquicheo (18°51′N, 100°48′W), 8 July 1970, E. Fisher, P. Sullivan (UCDC).

Diagnosis.—The medial teeth of the fixed chelal finger of *A. retrodentatus* are similar to *A. puebla* as both have strongly sinuate distal margins, unlike all other species of the genus. *Albiorix retrodentatus* differs from *A. puebla* in its larger size and in the position of trichobothrium ist_1, which is slightly dorso-distal to ist_3 in *A. retrodentatus* but is directly dorsal to ist_3 in *A. puebla*.

Description.—*Adult:* Color: pedipalps and carapace deep red-brown; chelicerae and legs yellow-brown; tergites and sternites pale yellow-brown.

Setae: generally long, straight and acicular.

Chelicera: hand with 6 setae; movable finger with 1 subdistal seta; galea very slender and elongate; fixed finger with 3 (male) medium teeth, plus 4 very small distal teeth; movable finger with 4 (male) teeth; rallum of 4 blades, each with several serrations; lamina exterior absent.

Pedipalp (Fig. 21B): trochanter with scattered granulations, strongest on retrolateral face, femur granulate on most faces, but strongest on prolateral surface, patella granulate on prolateral margin, chelal hand very sparsely granulate on prolateral margin at base of fingers; trochanter 2.10–2.57 (male), femur 4.01–4.08 (male), patella 2.71–3.10 (male), chela (with pedicel) 3.63–3.98 (male), chela (without pedicel) 3.44–3.78 (male), hand (without pedicel) 1.39–1.56 (male) x longer than broad, movable finger 1.44–1.50 (male) x longer than hand (without pedicel). Fixed chelal finger and hand with 22 trichobothria, movable chelal finger with 10 trichobothria (Fig. 21C): *eb*, *esb* and *isb* in straight row at base of finger; *eb*, *esb*, *isb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 4 trichobothria; *ist* region with 5 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus near *est* region in fixed finger and basal to *t* region in movable finger. Chelal hand with retrolateral condyle small and rounded. Chelal teeth evenly spaced and juxtadentate: fixed finger with 43–52 (male) low, retrorse teeth; movable finger with ca. 7–8 (male) low teeth; base of fixed chelal finger with several small denticles.

Carapace (Fig. 21A): lateral margins evenly convex; with 2 small bulging eyes; anterior margin medially prominent; with 20 setae including 4 setae on anterior margin and 4 on

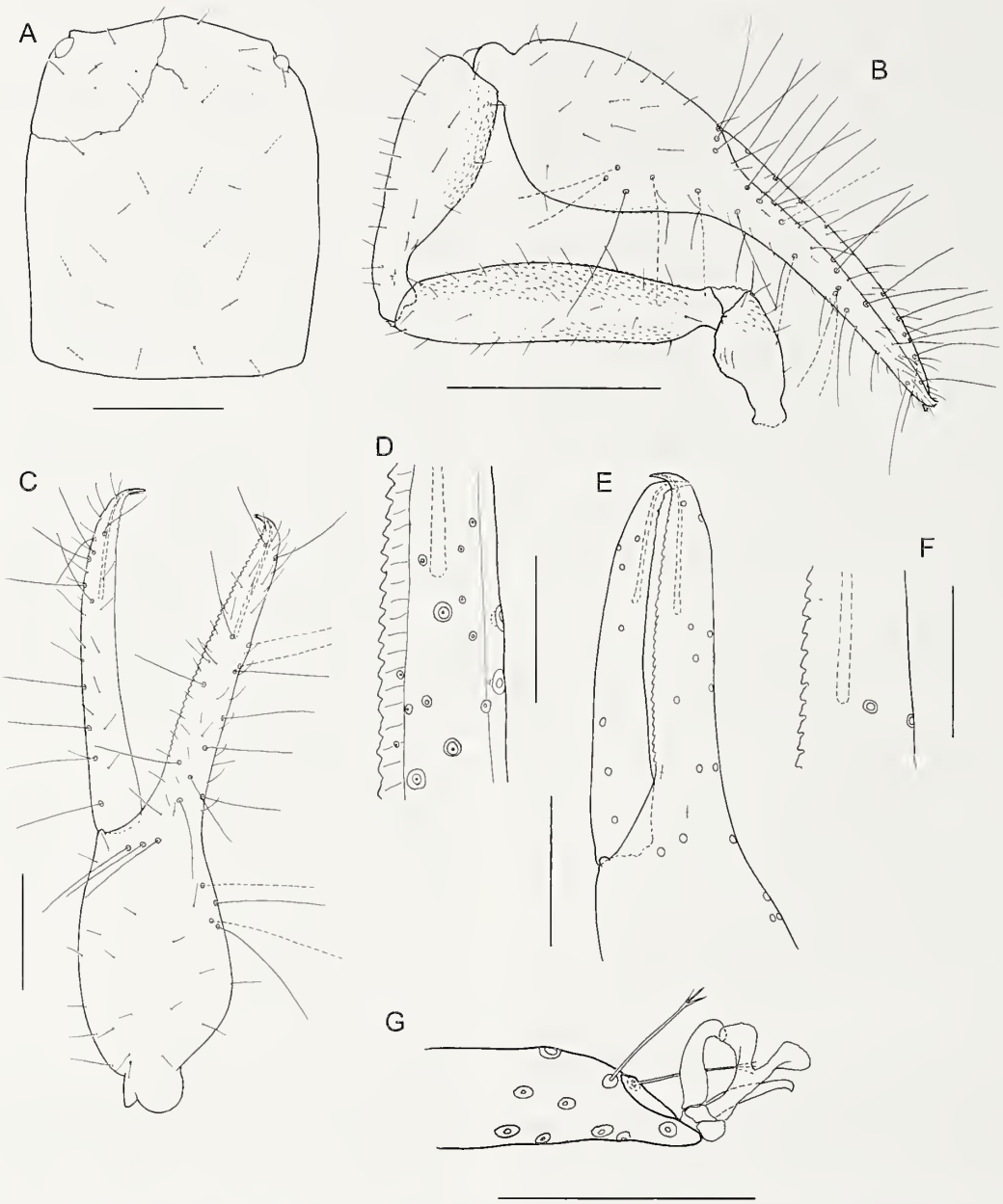

Figure 21.—*Albiorix retrodentatus* Hoff, male holotype, unless stated otherwise: A. Carapace, dorsal; B. Left pedipalp, dorsal; C. Left chela, lateral, male paratype; D. Detail of fixed chelal finger, male paratype; E. Left chela, tritonymph (UCDC); F. Detail of fixed chelal finger, tritonymph (UCDC); G. Tip of right tarsus IV, only subterminal tarsal setae shown. Scale lines = 0.5 mm (B, C); 0.25 mm (A); 0.2 mm (E); 0.1 mm (D, F, G).

posterior margin; with very faint posterior furrow situated close to posterior margin.

Coxal region: manducatory process somewhat pointed, with 2 long apical acuminate setae; chaetotaxy 2 + 8: 7: 7: 8: 7 (male).

Legs: femur + patella 2.26–2.62 (male) x longer than deep; subterminal tarsal setae trifurcate (Fig. 21G); arolium longer than claws, deeply divided (Fig. 21G).

Abdomen: tergites and sternites not divided; sclerites uniseriate. Tergal chaetotaxy: male, 4: 7: 8: 8: 8: 8: 8: 8: 8: 8: 9 (including 2 tactile setae): 2. Sternal chaetotaxy: male, 8: (1) 12 [3 + 3] (1): (1) 7 (1): 13: 12: 11: 11: 11: 10: 8 (including 4 tactile setae): 2. Setae of tergites and sternites IX–XI acuminate; with several tactile setae.

Genitalia: male with small dorsal apodeme; median genital deeply bipartite.

Dimensions (mm): Males: holotype followed by other males (where applicable): Body length 2.22 (2.35–2.61). Pedipalp: trochanter 0.326/0.155 (0.295–0.398/0.148–0.155), femur 0.784/0.192 (0.600–0.711/0.170–0.187), patella 0.650/0.210 (0.682–0.711/0.180–0.198), chela (with pedicel) 1.373/0.378 (1.065–1.448/0.320–0.370), chela (without pedicel) 1.301 (0.995–1.400), hand (without pedicel) length 0.525 (0.460–0.570), movable finger length 0.790 (0.770–0.848). Chelicera 0.301/0.156. Carapace 0.704/0.563 (0.651–0.720/0.503–0.611); eye diameter 0.078. Leg I: femur 0.0355/0.101, patella 0.193/0.095, tibia 0.296/0.063, metatarsus 0.167/0.051, tarsus 0.262/0.038. Leg IV: femur + patella 0.636/0.282 (0.620–0.675/0.265–

0.272), tibia 0.448/0.103, metatarsus 0.215/0.074, tarsus 0.339/0.050.

Tritonymph: Chelicera: galea long, slightly curved; hand with 6 setae, movable finger with 1 seta; rallum composed of 4 blades, all serrate.

Pedipalp: trochanter 1.99, femur 3.53, patella 3.79, chela (with pedicel) 3.33, chela (without pedicel) 3.11 × longer than broad. Fixed finger with 15 trichobothria, movable finger with 8 trichobothria (Fig. 21E); *eb*, *esb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 4 trichobothria; *ist* region with 3 trichobothria; *est* region with 4 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *st* region with 1 trichobothrium; *t* region with 5 trichobothria; *isb* and *sb* absent. Chelal hand with retrolateral condyle small and rounded.

Carapace: anterior margin medially prominent; 1 pair of small eyes present; with 21 setae including 4 setae on anterior margin and 4 setae on posterior margin.

Coxal region: posterior maxillary lyrifissure present, subbasal.

Legs: much as in adults.

Dimensions (mm): Body length 2.35. Pedipalp: trochanter 0.295/0.148, femur 0.600/0.170, patella 0.682/0.180, chela (with pedicel) 1.065/0.320, chela (without pedicel) 0.995, hand (without pedicel) length 0.460, movable finger length 0.550. Carapace 0.651/0.503.

Remarks.—*Albiorix retrodentatus* was described by Hoff (1945) from two males collected in Guerrero state, in southern Mexieo, but has rarely been mentioned since. Hoff (1956) identified two male specimens from Eddy County, New Mexico as *A. retrodentatus*. We have examined one of these specimens (from Whites City, erroneously called White City by Hoff) and found that it conforms very closely to specimens of *A. conodentatus* and that both samples were misidentified.

Beier (1963) described *A. bolivari* from a female holotype and six paratypes consisting of four males, a female and a tritonymph collected within Gruta de Acuitlapán, Guerrero, Mexico. We have had access to two of these male paratypes, which were slide-mounted by WBM. Beier (1963) justified *A. bolivari* as distinct from *A. magnus* based on several morphological differences and from *A. retrodentatus* on the slimmer pedipalpal segments. We find that while *A. bolivari* is indeed distinct from *A. conodentatus*, it cannot be easily separated from *A. retrodentatus*, with the chelae being nearly identical in size and shape. The type specimens of both species possess very eharacteristic teeth of the fixed chelal finger where the distal margins are sinuate, rather than straight. Hoff's (1945) description of *A. retrodentatus* included illustrations of the chelal teeth, but his Fig. 13 of the fixed finger failed to illustrate the sinuate shape. As we cannot find any other significant differences between the types of *A. retrodentatus* and *A. bolivari*, which were collected only 70 km from each other (Fig. 3C), we formally synonymize them, with *A. retrodentatus* taking priority over *A. bolivari*.

The tritonymph from Michoacan is tentatively associated with *A. retrodentatus*. The distal margins of the teeth of the fixed chelal finger are sinuate, but not strongly so, and may represent a different species. However, it was collected only 164 km from the type locality of *A. retrodentatus* and 133 km from the type locality of *A. bolivari*.

Albiorix retrodentatus is known only from a small region of southern Mexico, in the states of Guerrero and Michoacan (Fig. 3C).

Albiorix rosario Harvey & Muchmore sp. nov.
Figs. 3B, 22

Material examined.—*Holotype.* MEXICO: *Baja California:* male, 15 km E. of Rosario (30°04′N, 115°46′W), 7 February 1984–2 April 1985, pitfall trap, W.H. Clark (FSCA, WM7130.02001).

Diagnosis.—*Albiorix rosario* most closely resembles *A. edentatus* in having very low teeth of the fixed chelal finger that are much longer than high (Fig. 22D). It differs from *A. edentatus* in having bifurcate subterminal tarsal setae (Fig. 22E), and trichobothria *sb* and *st* situated much closer to each other than to b_2 (Fig. 22C).

Description.—*Adult:* Color: pedipalps, carapace and coxal region red-brown; abdomen pale red-brown; chelicera and legs light yellow-brown.

Setae: generally long, straight and acicular.

Chelicera: hand with 6 setae; movable finger with 1 subdistal seta; galea very slender and elongate; fixed finger with 3 (male) small teeth; movable finger with 2 (male) very small teeth; rallum of 4 blades, each with several serrations; lamina exterior absent.

Pedipalp (Figs. 22B, 22C): trochanter with scattered granulations, femur coarsely granulate on prolateral face and lightly granulate on retrolateral face, more prominent in basal half, and patella lightly granulate on prolateral face, chelal hand lightly granulate on prolateral surface at base of fingers, but smooth on retrolateral face; trochanter ? (damaged), femur 3.95 (male), patella 2.99 (male), chela (with pedicel) ? (poorly oriented), chela (without pedicel) ? (poorly oriented), hand (without pedicel) ? (poorly oriented) x longer than broad, movable finger 1.54 (male) x longer than hand (without pedicel). Fixed chelal finger and hand with 20 trichobothria, movable chelal finger with 10 trichobothria (Fig. 22C): *eb*, *esb* and *isb* in straight row at base of finger; *eb*, *esb*, *isb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 4 trichobothria; *ist* region with 5 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus within *est* region in fixed finger and at base of *t* region in movable finger. Chelal hand with retrolateral condyle small and rounded. Chelal teeth evenly spaced and juxtadentate: fixed finger with 29 (male) very low, retrorse teeth, each much longer than high; movable finger without any obvious teeth; base of fixed chelal finger with several small denticles.

Carapace (Fig. 22A): lateral margins evenly convex; 1.25 (male) x longer than broad; with 2 small bulging eyes; anterior margin medially prominent; with 20 (male) setae including 4 setae on anterior margin and 4 on posterior margin; with very faint posterior furrow situated close to posterior margin.

Coxal region: manducatory process somewhat pointed, with 2 long apical acuminate setae; chaetotaxy 2 + 7: 5: 5: 5: 6 (male).

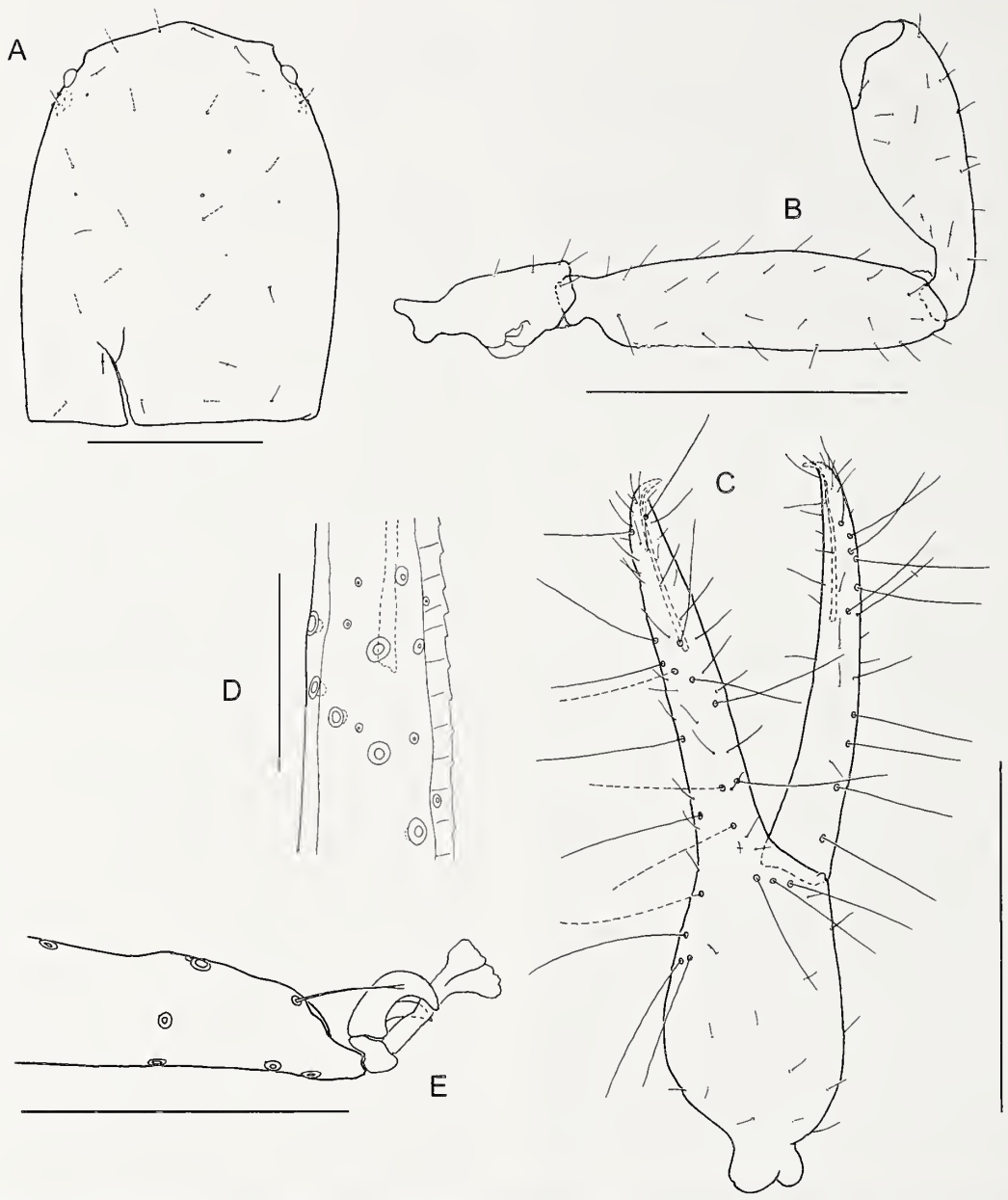

Figure 22.—*Albiorix rosario* Harvey & Muchmore sp. nov., male holotype: A. Carapace, dorsal; B. Right pedipalp, except chela, dorsal; C. Right chela, lateral; D. Detail of fixed chelal finger; E. Tip of right tarsus IV, only subterminal tarsal seta shown. Scale lines = 0.5 mm (A, B, C); 0.1 mm (D, E).

Legs: femur + patella 2.20 (male) x longer than deep; subterminal tarsal setae bifurcate, each tine short (Fig. 22E); arolium longer than claws, deeply divided (Fig. 22E).

Abdomen: tergites and sternites not divided; sclerites uniseriate, except for sternite II, which has scattered setae. Tergal chaetotaxy: male, 4: 4: 5: 8: 6: 6: 8: 6: 6: 8 (including 2 tactile setae): 7 (including 4 tactile setae): 2. Sternal chaetotaxy: male, 8: (1) 8 [2 + 3] (1): (1) 6 (1): 9: 9: 8: 9: 7: 6: 7 (including 3 tactile setae): 2. Setae of tergites and sternites IX–XI acuminate; with several tactile setae.

Genitalia: male with small dorsal apodeme; median genital sac bipartite.

Dimensions (mm): Male: holotype: Body length 1.94. Pedipalp: trochanter 0.280/? (damaged), femur 0.609/0.154, patella 0.479/0.160, chela (with pedicel) 1.021/? (poorly oriented), chela (without pedicel) 0.941, hand (without pedicel) length 0.385, movable finger length 0.592. Chelicera 0.223/0.112; movable finger length 0.132. Carapace 0.570/0.455; eye diameter 0.032. Leg I: femur 0.269/0.082, patella 0.147/0.077, tibia 0.214/0.054, metatarsus 0.188/0.044, tarsus 0.177/0.034. Leg IV: femur + patella 0.466/0.212, tibia 0.327/0.090, metatarsus 0.154/0.064, tarsus 0.230/0.044.

Remarks.—The holotype and only known specimen of *A. rosario* is missing the left pedipalp, and the right chela is mounted in a lateral view. Therefore, it is not possible to calculate the width of the chelal hand.

Albiorix rosario has only been found at a single location in northern Baja California, Mexico (Fig. 3B).

Etymology.—The specific epithet is a noun in apposition based on the type locality, El Rosario.

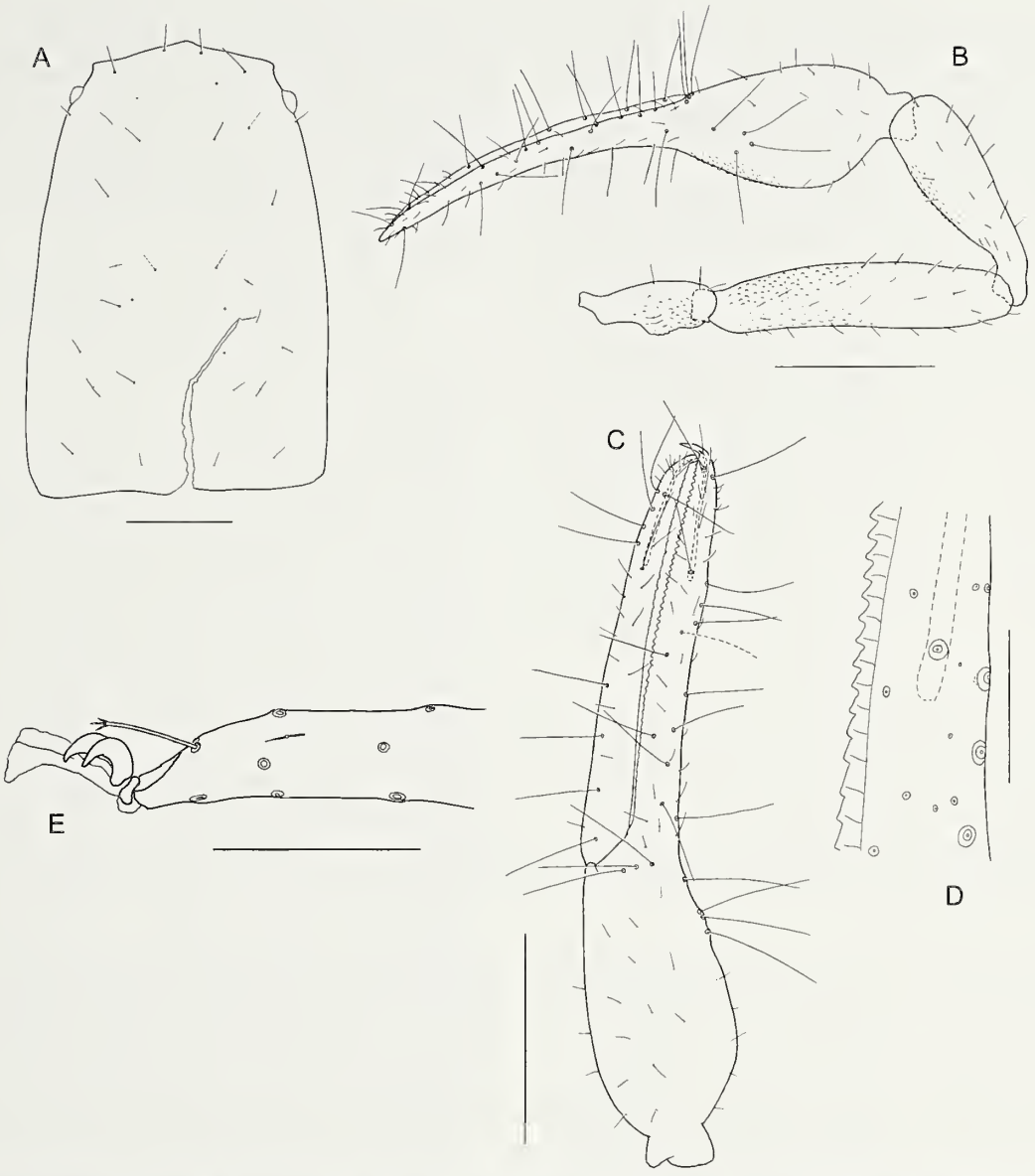

Figure 23.—*Albiorix sarahae* Harvey & Muchmore sp. nov., male holotype: A. Carapace, dorsal; B. Right pedipalp, dorsal; C. Left chela, lateral; D. Detail of fixed chelal finger; E. Tip of right tarsus IV, only subterminal tarsal seta shown. Scale lines = 0.5 mm (B, C); 0.2 mm (A); 0.1 mm (D, E).

Albiorix sarahae Harvey & Muchmore sp. nov.
Figs. 3A, 23

Material examined.—*Holotype*. USA: *California*: male, San Bernardino County, Soda Lake Zzyxx Field Station (35°10.323′N, 116°06.596′W), 12–14 April 2005, under rocks on hillside, S. Crews (CAS).

Paratype. USA: *California*: 1 female, Inyo County, Death Valley National Park, Highway 178, 1.8 miles E. of Salsberry Gap (35°56.961′N, 116°24.793′W), 1,270 feet, 23 September 2001, rocky alluvial fan, M. Hedin, S. Crews, J. Starrett (CAS).

Diagnosis.—*Albiorix sarahae* most closely resembles *A. vigintus* and *A. gertschi* in the position of trichobothrium ib_5 which is displaced distally. It differs from both these species by the presence of 21 trichobothria, in which the missing trichobothrium is ist_1.

Description.—*Adult:* Color: pedipalps, coxae and carapace deep yellow-brown, legs and chelicerae pale yellow-brown.

Setae: generally long, straight and acicular.

Chelicera: hand with 6 setae; movable finger with 1 subdistal seta; galea very slender and elongate; fixed finger with 4 (male), 6 (female) small teeth; movable finger with 5 (male), 4 (female) teeth; rallum of 4 blades, each with several serrations; lamina exterior absent.

Pedipalp (Fig. 23B): trochanter with scattered granulations, more prominent on retrolateral margins, femur coarsely granulate on prolateral surface, lightly granulate elsewhere, patella lightly granulate on prolateral surface, chelal hand lightly granulate on prolateral and retrolateral surface at base of fingers; trochanter 2.51 (male), 2.53 (female), femur 5.08 (male), 4.37 (female), patella 3.40 (male), 3.06 (female), chela

(with pedicel) 4.37 (male), 3.69 (female), chela (without pedicel) 4.16 (male), 3.50 (female), hand (without pedicel) 1.58 (male), 1.43 (female) x longer than broad, movable finger 1.67 (male), 1.46 (female) x longer than hand (without pedicel). Fixed chelal finger and hand with 21 trichobothria, movable chelal finger with 10 trichobothria (Fig. 23C): *eb*, *esb* and *isb* in straight row at base of finger; *eb*, *esb*, *isb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 4 trichobothria, ib_5 displaced distally in advance of *eb*, *esb* and *isb*; *ist* region with 6 trichobothria, ist_1 absent; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus at distal end of *est* region in fixed finger and basal to *t* region in movable finger. Chelal hand with retrolateral condyle small and rounded. Chelal teeth evenly spaced and juxtadentate: fixed finger with 53 (male), 44 (female) low, retrorse teeth; movable finger with 10 (male), 6 (female) obvious, low teeth, followed by additional very low teeth; base of fixed chelal finger with several small denticles.

Carapace (Fig. 23A): lateral margins evenly convex; with 2 small bulging eyes; anterior margin medially prominent; with 24 (male), 22 (female) setae including 4 setae on anterior margin and 4 on posterior margin; with very faint posterior furrow situated close to posterior margin.

Coxal region: manducatory process somewhat pointed, with 2 long apical acuminate setae; ehaetotaxy 2 + 8: 4: 5: 5: 7 (male); 2 + 8: 5: 5: 5: 6 (female).

Legs: femur + patella 2.71 (male), 2.87 (female) x longer than deep; subterminal tarsal setae trifurcate (Fig. 23E); arolium longer than claws, deeply divided (Fig. 23E).

Abdomen: tergites and sternites not divided; sclerites uniseriate. Tergal chaetotaxy: male, 4: 4: 6: 6: 6: 6: 6: 8: 8: 8: 8 (including 4 tactile setae): 2; female, 4: 4: 4: 8: 8: 8: 8: 9: 8: 7: 8 (including 4 tactile setae): 2. Sternal chaetotaxy: male, 6: (1) 13 [3 + 3] (1): (1) 6 (1): 12: 10: 10: 9: 10: 8: 5 (including 3 tactile setae): 2; female, 6: (1) 6 (1): (1) 8 (1): 10: 10: 9: 9: 8: 9: 10 (including 4 tactile setae): 2; setae of anterior genital operculum (sternite II) of female very small. Setae of tergites and sternites IX–XI acuminate; with several tactile setae.

Genitalia: male with small dorsal apodeme; median genital sac bipartite; female with large gonosac, which is covered with scattered pores.

Dimensions (mm): Males: holotype: Body length 2.22. Pedipalp: trochanter 0.402/0.160, femur 1.000/0.197, patella 0.720/0.212, chela (with pedicel) 1.660/0.380, chela (without pedicel) 1.580, hand (without pedicel) length 0.600, movable finger length 1.003. Chelicera 0.323/0.142, movable finger length 0.190. Carapace 0.845/0.555; eye diameter 0.040. Leg I: femur 0.461/0.109, patella 0.261/0.098, tibia 0.360/0.065, metatarsus 0.207/0.050, tarsus 0.305/0.038. Leg IV: femur + patella 0.752/0.277, tibia 0.543/0.111, metatarsus 0.255/0.077, tarsus 0.390/0.050.

Female: paratype: Body length 2.08. Pedipalp: trochanter 0.418/0.165, femur 0.895/0.205, patella 0.700/0.229, chela (with pedicel) 1.590/0.431, chela (without pedicel) 1.507, hand (without pedicel) length 0.618, movable finger length 0.900. Chelicera 0.330/0.158, movable finger length 0.188. Carapace 0.792/0.540; eye diameter 0.040. Leg I: femur 0.425/0.103, patella 0.215/0.092, tibia 0.321/0.064, metatarsus 0.180/0.054, tarsus 0.387/0.041. Leg IV: femur + patella 0.700/0.244, tibia 0.502/0.109, metatarsus 0.251/0.070, tarsus 0.380/0.048.

Remarks.—This species is known from two localities situated in the Mojave Desert in eastern California (Fig. 3A).

Etymology.—This species is named for Sarah Crews, who collected both specimens.

Albiorix vigintus Harvey & Muchmore sp. nov.
Figs. 3A, 24

Albiorix mexicanus Chamberlin 1930:45 (in part, specimen from Nevada).

Material examined.—*Holotype*. USA: *Utah*: male, Saint George, Washington County (37°06′N, 113°35′W), 26 April 1935, G.F. Knowlton, C.F. Smith (CAS, JC–1069.01001).

Paratypes. USA: *Arizona*: 2 males, 3 miles N., 7 miles E. of Littlefield, Virgin River, Mohave County (36°57′N, 113°48′W), 28 March–1 October 1982, D. Giuliani (FSCA, WM7705); *Nevada*: 1 male, Newberry Mts. at Pipe Springs Road junction, Clark County (35°16′N, 114°41′W), 28 September–7 October 1994, *Larrea* desert, W.L. Pratt (CAS); *Utah*: 1 male, collected with holotype (CAS, JC–1069.01002); 1 male, 2 miles E. of Washington, Washington County (37°08′N, 113°26′W), 20 May–8 June 1980, pit trap, sandy sagebrush and creosote area, R. Hardy (FSCA, WM5805.01001); 1 female, Saint George, Washington County (37°06′N, 113°35′W), 19 March 1924, V.M. Tanner (CAS, JC–245.01001).

Diagnosis.—*Albiorix vigintus* most closely resembles *A. gertschi* and *A. sarahae* in having trichobothrium ib_5 situated distally (Fig. 24A), but unlike these two species, which have 22 and 21 trichobothria on the fixed chelal finger and hand, respectively, it has only 20 trichobothria with only 4 trichobothria in the *ist* group (Figs. 24A, 24B).

Description.—*Adult:* Color: pedipalps, coxae and carapaee deep yellow-brown, legs and chelicerae pale yellow-brown.

Setae: generally long, straight and acicular.

Chelicera: hand with 6 setae; movable finger with 1 subdistal seta; galea very slender and elongate; fixed finger with 5 (male), 6 (female) small teeth; movable finger with 5 (male), 5 (female) teeth; rallum of 4 blades, each with several serrations; lamina exterior absent.

Pedipalp (Fig. 24A): trochanter with scattered granulations, femur coarsely granulate on most faces, more strongly granulate on prolateral face, patella coarsely granulate on prolateral face, chelal hand lightly granulate on prolateral and retrolateral surfaces at base of fingers; trochanter 2.18–2.37 (male), 2.41–2.50 (female), femur 4.43–4.82 (male), 4.39–4.67 (female), patella 2.85–3.67 (male), 3.30–3.58 (female), chela (with pedicel) 3.92–4.18 (male), 3.78–4.13 (female), chela (without pedicel) 3.75–3.95 (male), 3.69–3.93 (female), hand (without pedicel) 1.54–1.63 (male), 1.49–1.59 (female) x longer than broad, movable finger 1.39–1.55 (male), 1.45–1.61 (♀female) x longer than hand (without pedicel). Fixed chelal finger and hand with 20 trichobothria, movable chelal finger with 10 trichobothria (Fig. 24B): *eb*, *esb* and *isb* in straight row at base of finger; *eb*, *esb*, *isb*, *it* and *et* regions each with 1 trichobothrium; *ib* region with 5 trichobothria, ib_5 displaced

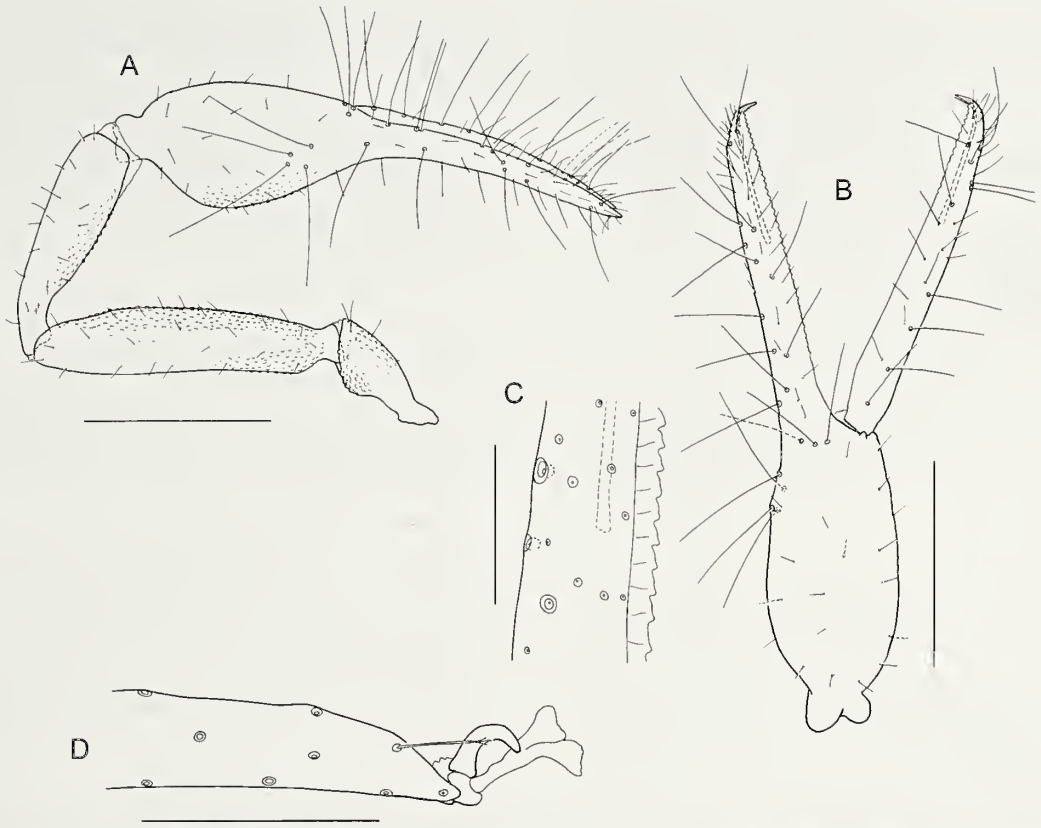

Figure 24.—*Albiorix vigintus* Harvey & Muchmore sp. nov., male holotype: A. Left pedipalp, dorsal; B. Right chela, lateral; C. Detail of fixed chelal finger; D. Tip of right tarsus IV, only subterminal tarsal seta shown. Scale lines = 0.5 mm (A, B); 0.1 mm (C, D).

distally in advance of *eb*, *esb* and *isb*; *ist* region with 4 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *sb* and *st* regions each with 1 trichobothrium; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus within *est* region in fixed finger and basal to *t* region in movable finger. Chelal hand with retrolateral condyle small and rounded. Chelal teeth evenly spaced and juxtadentate: fixed finger with 39–52 (male), 50–54 (female) low, retrorse teeth (Fig. 24C); movable finger with ca. 9–16 (male), 12–15 (female) obvious, low teeth, followed by additional very low teeth; base of fixed chelal finger with several small denticles.

Carapace: lateral margins evenly convex; with 2 small bulging eyes; anterior margin medially prominent; with 22–25 (male), 22 (female) setae including 4 setae on anterior margin and 4 (occasionally 3) on posterior margin; with very faint posterior furrow situated close to posterior margin.

Coxal region: manducatory process somewhat pointed, with 2 long apical acuminate setae; chaetotaxy 2 + 7: 6: 7: 6: 7 (male); 2 + 7: 5: 6: 5: 6 (female).

Legs: femur + patella 2.25–2.38 (male), 2.73–2.77 (female) x longer than deep; subterminal tarsal setae trifurcate (Fig. 24D); arolium longer than claws, deeply divided (Fig. 24D).

Abdomen: tergites and sternites not divided; sclerites uniseriate, except for male sternites II and III where the setae are scattered. Tergal chaetotaxy: holotype male, 4: 5: 5: 6: 7: 7: 8: 8: 6: 8 (including 4 tactile setae): 7 (including 4 tactile setae): 2; female, 3: 4: 5: 6: 7: 8: 6: 6: 6: 6 (including 2 tactile setae): 7 (including 4 tactile setae): 2. Sternal chaetotaxy: holotype male, 6: (1) 11 [3 + 3] (1): (1) 7 (1): 8: 9: 8: 9: 9: 8: 8 (including 4 tactile setae): 2; female, 6: (1) 6 (1): (1) 6 (1): 8: 8: 8: 8: 7: 8: 8 (including 4 tactile setae): 2; setae of anterior genital operculum (sternite II) of female very small. Setae of tergites and sternites IX–XI acuminate; with several tactile setae.

Genitalia: male with small dorsal apodeme; median genital sac bipartite; female with large gonosac, which is covered with scattered pores.

Dimensions (mm): Males: holotype followed by other males (where applicable): Body length 2.46 (1.73–2.68). Pedipalp: trochanter 0.367/0.157 (0.294–0.371/0.135–0.161), femur 0.834/0.173 (0.773–0.856/0.170–0.180), patella 0.635/0.173 (0.493–0.654/0.173–0.186), chela (with pedicel) 1.376/0.340 (1.328–1.472/0.339–0.352), chela (without pedicel) 1.320 (1.270–1.392), hand (without pedicel) length 0.554 (0.522–0.574), movable finger length 0.768 (0.760–0.835). Chelicera 0.309/0.156; movable finger length 0.184. Carapace ?/? (damaged) (0.603–0.708/?); eye diameter 0.038. Leg I: femur 0.400/0.099, patella 0.201/0.087, tibia 0.312/0.061, metatarsus 0.167/0.049, tarsus 0.253/0.040. Leg IV: femur + patella 0.656/0.291 (0.653/0.274), tibia 0.460/0.111, metatarsus 0.231/0.070, tarsus 0.333/0.045.

Females: paratype (JC–245.01001) followed by other females (where applicable): Body length 2.65 (1.76–2.45). Pedipalp: trochanter 0.420/0.168 (0.380–0.388/0.158–0.157), femur 0.941/0.202 (0.835–0.920/0.190–0.197), patella 0.686/

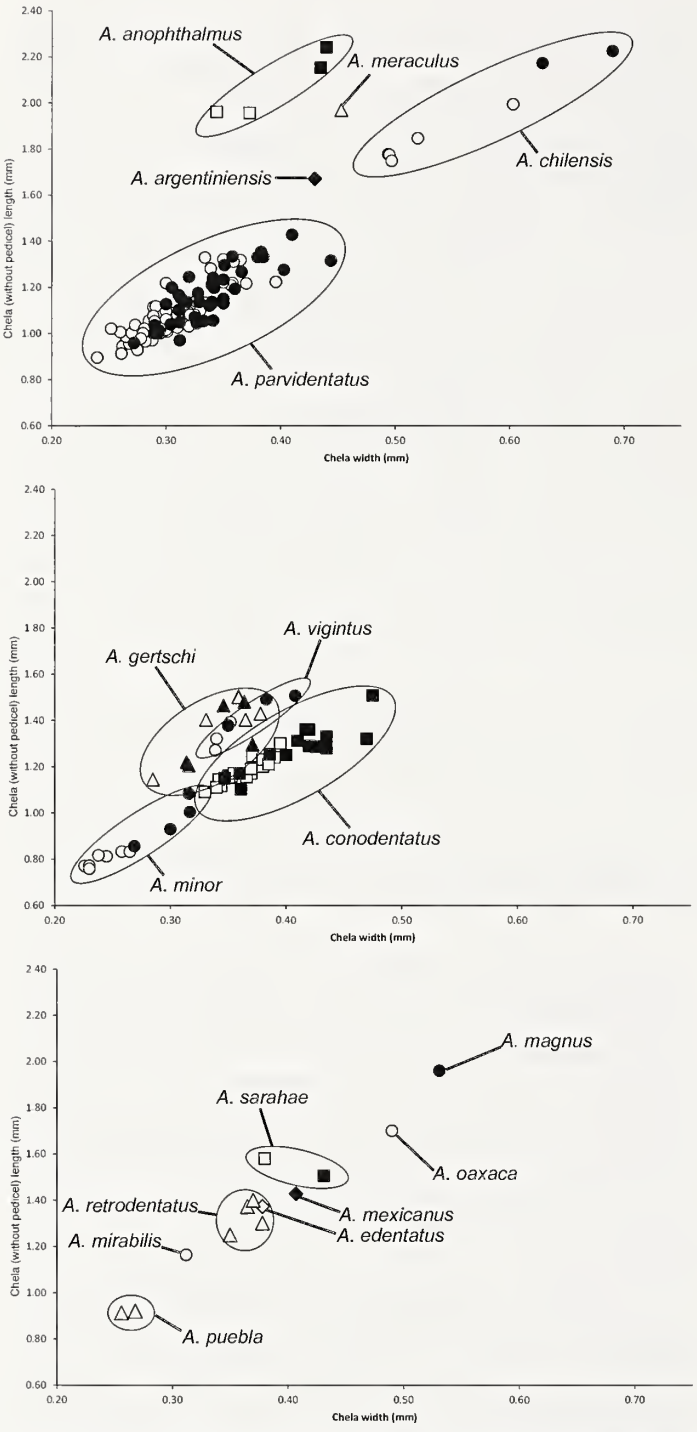

Figure 25.—Graph depicting chela (without pedicel) length versus chela width, for all *Albiorix* spp. except *A. rosario* Harvey & Muchmore sp. nov. as the sole specimen has the chela mounted laterally.

0.196 (0.610–0.681/0.185–0.190), chela (with pedicel) 1.544/0.408 (but slightly damaged and flattened) (1.446–1.556/0.350–0.383), chela (without pedicel) 1.506 (1.377–1.490), hand (without pedicel) length 0.616 (0.555–0.571), movable finger length 0.896 (0.825–0.917). Chelicera 0.344/0.168, movable finger length 0.205. Carapace 0.778/? (damaged) (0.740–0.743/0.504–0.524); eye diameter 0.045. Leg I: femur 0.422/0.109, patella 0.208/0.097, tibia 0.331/0.066, metatarsus 0.181/0.057, tarsus 0.275/0.040. Leg IV: femur + patella 0.701/0.257 (0.710/0.256), tibia 0.481/0.104, metatarsus 0.243/0.071, tarsus 0.352/0.051.

Remarks.—This species is known from a small area of the Rocky Mountains in south-western Utah, southern Nevada and north-western Arizona (Fig. 3A).

Etymology.—The specific epithet refers to the presence of only 20 trichobothria on the fixed chelal finger and hand (*viginti*, Latin, twenty).

Genus *Ideoroncus* Balzan 1887

Ideoroncus Balzan 1887: no pagination; Balzan 1890:443–444; Chamberlin 1930:44; Beier 1932a:171–172; Mahnert 1984a:653; Harvey 1991:319; Harvey 2013:unpaginated.

Ideobisium (Ideoroncus) Balzan: Balzan 1892:540; With 1906:81.

Type species.—*Ideoroncus pallidus* Balzan 1887, by monotypy.

Diagnosis.—Species of *Ideoroncus* differ from all other ideoroncid genera by the dorsal displacement of trichobothrium *sb* on the movable chelal finger.

Description.—*Adult:* setae: long, straight and acicular.

Chelicera: hand with 5 or occasionally 6 setae; movable finger with 1 long subdistal seta; rallum of 4 thickened blades, all blades serrate; lamina exterior absent; galea long and slender.

Pedipalps: long and slender. Patella with disto-prolateral excavation. Fixed chelal finger and hand with 20 or 21 trichobothria (rarely 22), movable chelal finger with 10 trichobothria: *eb* region with 1 trichobothrium; *est* region with 6 trichobothria; *ib* region with 4 trichobothria; *ist* region with 5 or 6 trichobothria; *b* region with 2 trichobothria; *sb* and *st* regions with 1 trichobothrium; and *t* region with 6 trichobothria; *sb* dorsally displaced relative to *st*; *st* not ventrally displaced. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus distal to *est* region in fixed finger and near *t* region in movable finger. Chelal teeth small and evenly spaced; base of fixed chelal finger with several small denticles. Chelal hand with retrolateral condyle small and rounded.

Carapace: with 2 small, bulging eyes, or eyes absent; with or without basal furrow; anterior margin with 6, or occasionally 4 or 8 setae.

Coxal region: manducatory process with 2 long distal setae. Median maxillary lyrifissure present and sub-basally situated.

Legs: femur I and II without basal swelling; femora I and II with primary slit sensillum directed transversely; femur I much longer than patella I; suture line between femur IV and patella IV transverse; metatarsus shorter than tarsus; metatarsal pseudotactile seta sub-proximal; legs with dentate subterminal tarsal setae; arolium about as long as the claws, not divided, without ventral hooked protuberance; without sub-ungual spine; claws slender and simple.

Abdomen: tergites undivided; sternites with faint medial suture line. Pleural membrane longitudinally striate. Each stigmatic sclerite with 1 seta; spiracles simple, with spiracular helix. Anterior margin of anal operculum not abutting posterior margin of sternite X.

Genitalia: male median genital sac bipartite; female with large gonosac covered with scattered pores.

Tritonymph: Pedipalps: fixed finger with 14 trichobothria, movable finger with 8 trichobothria; *eb* region with 1 trichobothrium; *ib* region with 4 trichobothria; *ist* region with 3 trichobothria; *est* region with 4 trichobothria; *et* distal to *it*; *b* region with 2 trichobothria; *t* region with 5 trichobothria; *isb* and *st* absent.

Deutonymph: Pedipalps: fixed finger with 9 trichobothria, movable finger with 6 trichobothria; *eb* region with 1 trichobothrium; *ib* region with 2 trichobothria; *ist* region with 2 trichobothria; *est* region with 2 trichobothria; *et* distal to *it*; *b* region with 2 trichobothria; *t* region with 4 trichobothria; others absent.

Protonymph: Pedipalps: *eb*, *et*, *ist* and *t* regions each with 1 trichobothrium; others absent.

Remarks.—The genus *Ideoroncus* is currently known from nine species distributed in Paraguay and southern Brazil (Mahnert 1984a, 2001; Harvey 2013) (Figs. 2B, 26A, 27B).

KEY TO SPECIES OF *IDEORONCUS* (ADAPTED FROM MAHNERT 1984A)

1. Eyes present 2
   Eyes absent 8
2. Fixed chelal finger and hand with 20 trichobothria, including *ist* region with 5 trichobothria 3
   Fixed chelal finger and hand with 21 trichobothria, including *ist* region with 6 trichobothria 6
3. Eyes small ..... *I. pallidus*
   Eyes large 4
4. Carapace with subbasal thickened band 5
   Carapace without subbasal thickened band ..... *I. paranensis*
5. Pedipalpal femur 0.49 (male), 0.51 (female) mm in length; 3.5–3.9 × longer than broad; pedipalpal tibia 2.5–2.8 × longer than broad; tergite IX with 9–11 setae ..... *I. lenkoi*
   Pedipalpal femur at least 0.51 (msle), 0.58 (female) mm in length; 3.8–4.3 × longer than broad; pedipalpal tibia 2.7–3.0 × longer than broad; tergite IX with 13–15 setae ..... *I. setosus*
6. Smaller and slightly thicker appendages, e.g. pedipalpal femur of male 0.55–0.63 mm, of female 0.65–0.77 mm long, and 3.7–4.1 × longer than broad 7
   Larger and thinner appendages, e.g. pedipalpal femur of male 0.70–0.72 mm long, and 4.5 × longer than broad ..... *I. procerus*
7. Pedipalps uniformly yellow-brown; carapace and tergites brown; tergite IX with 11–15 setae; pedipalpal femur 3.7–4.1 × longer than broad ..... *I. divisus*
   Pedipalps red brown, hand slightly darker; carapace and tergites dark chocolate brown; tergite IX with 8–11 setae; pedipalpal femur 3.8–3.9 × longer than broad ..... *I. beieri*
8. Pedipalps slender, e.g., pedipalpal femur 5.5–5.7 × longer than broad ..... *I. cavicola*
   Pedipalps less slender, e.g., pedipalpal femur 3.3 × longer than broad ..... *I. anophthalmus*

Ideoroncus anophthalmus Mahnert 1984
(Fig. 26A)

Ideoroncus anophthalmus Mahnert 1984a:663–665, figs 22–24; Harvey 1991:319; Harvey 2013:unpaginated.

Material examined.—None.

Diagnosis.—*Ideoroncus anophthalmus* resembles *I. cavicola* in the lack of eyes, but differs in having less slender appendages; e.g., pedipalpal femur 3.3 × longer than broad, compared with 5.5–5.7 × in *I. cavicola*.

Description.—*Adults:* See Mahnert (1984a).

Remarks.—This species only occurs in São Paulo state, Brazil (Mahnert 1984a) (Fig. 26A).

Ideoroncus beieri Mahnert 1984
Fig. 26B

Ideoroncus lenkoi Beier: Beier 1974:899 (misidentification, in part).
Ideoroncus beieri Mahnert 1984a:668–670, figs 34–37; Harvey 1991:319; Harvey 2013:unpaginated.

Material examined.—None.

Diagnosis.—*Ideoroncus beieri* resembles *I. procerus* and *I. divisus* in having 21 trichobothria on the fixed chelal finger and hand, but has much darker pedipalps, carapace and tergites, and slightly different pedipalpal ratios.

Description.—*Adult:* See Mahnert (1984a).

Remarks.—*Ideoroncus beieri* occurs in Paraná state, Brazil (Mahnert 1984a) (Fig. 26B).

Ideoroncus cavicola Mahnert 1984
Fig. 26A

Ideoroncus cavicola Mahnert 2001:103–106, figs 17–21.

Material examined.—None.

Diagnosis.—*Ideoroncus cavicola* resembles *I. anophthalmus* in the lack of eyes, but differs in having more slender appendages; e.g., pedipalpal femur 5.5–5.7 × longer than broad, compared with 3.3 × in *I. anophthalmus*.

Description.—*Adult:* See Mahnert (1984a, 2001).

Remarks.—*Ideoroncus cavicola* is known from caves in the Iporanga district of São Paulo state, Brazil (Mahnert 2001) (Fig. 26A).

Ideoroncus divisus Mahnert 1984
Fig. 26B

Ideoroncus pallidus Balzan: Beier 1974:899 (misidentification).
Ideoroncus divisus Mahnert 1984: 666–668, Figs. 29–33; Harvey 1991:319; Harvey & Volschenk 2007:368, Figs. 1–4; Harvey 2013:unpaginated.

Material examined.—*Paratypes*. **Brazil:** *Santa Catarina*: 1 ♂, Nova Teutonia [27°03′S, 52°24′W], January 1965, F. Plau-

mann (WAM T90/1164); 1 ♀, same data except June 1957 (WAM T90/1165).

Diagnosis.—*Ideoroncus divisus* resembles *I. procerus* and *I. beieri* in having 21 trichobothria on the fixed chelal finger and hand, but has smaller and slightly thicker pedipalpal segments than *I. procerus*, and has lighter colored pedipalps, carapace and tergites, and more setae on tergite IX than *I. beieri*.

Description.—*Adult:* See Mahnert (1984a).

Nymphs: See Mahnert (1984a).

Remarks.—This species is known from the Brazilian states of Rio Grande do Sul and Santa Catarina (Mahnert 1984a) (Fig. 26B).

Ideoroncus lenkoi Beier 1970
Fig. 26B

Ideoroncus lenkoi Beier 1970:55–56, Fig. 3; Beier 1974:899 (in part; see *Ideoroncus beieri* Mahnert); Mahnert 1984a:655–656, Figs. 3–7; Harvey 1991:319; Harvey et al. 2007:Fig. 4; Harvey 2013:unpaginated.

Ideoroncus aff. *lenkoi* Beier: Mahnert 1984a:657.

Not *Ideoroncus lenkoi* Beier: Beier 1974:899 (misidentification, in part; see *Ideoroncus beieri* Mahnert and *I. paranensis* Mahnert).

Material examined.—BRAZIL: *São Paulo:* São Sebastiao, Station Biologique (23°49′S, 45°27′W), 25 June 1960, Buchswald, R. Schuster (WAM T90/1166–1167).

Diagnosis.—*Ideoroncus lenkoi* resembles *I. anophthalmus*, *I. cavicola*, *I. pallidus*, *I. paranensis* and *I. setosus* in having 20 trichobothria on the fixed chelal finger and hand, but has larger eyes, unlike *I. anophthalmus* and *I. cavicola* which are eyeless, and *I. pallidus*, which has very small eyes, has a thickened subbasal band on the carapace not found in *I. paranensis*, and the high number of setae (13–15) on tergite IX found in *I. setosus*.

Description.—*Adult:* See Mahnert (1984a).

Nymphs: See Mahnert (1984a).

Remarks.—This species was originally described from São Paulo state, Brazil, and redescribed by Mahnert (1984a) (Fig. 26B).

Ideoroncus pallidus Balzan 1887
Fig. 26A

Ideoroncus pallidus Balzan 1887: no pagination, figs; Balzan 1890:444–445, Figs. 23, 23a–b; Chamberlin 1930:44; Beier 1932a:171, Fig. 201; Roewer 1937:257; Mahnert 1984a:653–655, Figs. 1–3; Harvey 1991:319; Harvey 2013:unpaginated.

Ideobisium (Ideoroncus) pallidum (Balzan): Balzan 1892:541, 549.

Ideobisium pallidum (Balzan): Ellingsen 1910:395.

Not *Ideoroncus pallidus* Beier: Beier 1974:899 (misidentification; see *Ideoroncus divisus* Mahnert).

Material examined.—None.

Diagnosis.—*Ideoroncus pallidus* resembles *I. anophthalmus*, *I. cavicola*, *I. lenkoi*, *I. paranensis* and *I. setosus* in having 20 trichobothria on the fixed chelal finger and hand, but has very small eyes, unlike *I. anophthalmus* and *I. cavicola*, which are eyeless, and *I. lenkoi*, *I. paranensis* and *I. setosus*, which have larger eyes.

Description.—*Adult:* See Mahnert (1984a).

Remarks.—*Ideoroncus pallidus* is known only from the type material collected at Rio Apa, Paraguay (Fig. 26A). The status of the specimens from Brazil as *Ideobisium pallidum* by (Ellingsen 1910) is unknown.

Ideoroncus paranensis Mahnert 1984
Fig. 26A

Ideoroncus lenkoi Beier: Beier 1974:899 (misidentification, in part).

Ideoroncus paranensis Mahnert 1984: 657–659, Figs. 8–14; Harvey 1991:320; Harvey 2013:unpaginated.

Material examined.—None.

Diagnosis.—*Ideoroncus paranensis* resembles *I. anophthalmus*, *I. cavicola*, *I. lenkoi*, *I. pallidus* and *I. setosus* in having 20 trichobothria on the fixed chelal finger and hand, but has larger eyes, unlike *I. anophthalmus* and *I. cavicola*, which are eyeless, and *I. pallidus*, which has very small eyes, and lacks a thickened subbasal band on the carapace found in *I. lenkoi* and *I. setosus*.

Description.—*Adult:* See Mahnert (1984a).

Nymphs: See Mahnert (1984a).

Remarks.—*Ideoroncus paranensis* has only been collected from Paraná state, Brazil (Mahnert 1984a) (Fig. 26A).

Ideoroncus procerus Beier 1974
Fig. 26A

Ideoroncus procerus Beier 1974:900–901, Fig. 1; Mahnert 1984a:665–666, Figs. 25–28; Harvey 1991:320; Harvey 2013:unpaginated.

Material examined.—None.

Diagnosis.—*Ideoroncus procerus* resembles *I. setosus* and *I. beieri* in having 21 trichobothria on the fixed chelal finger and hand, but is larger with a pedipalpal femur length of 0.70–0.72 (male), compared with at most 0.63 mm in *I. setosus* and *I. beieri*.

Description.—*Adult:* See Mahnert (1984a).

Remarks.—*Ideoroncus procerus* was originally described from Nova Teutônia, Santa Catarina state, Brazil (Beier 1974) (Fig. 26A) and redescribed by Mahnert (1984a).

Ideoroncus setosus Mahnert 1984
Fig. 26A

Ideoroncus setosus Mahnert 1984:659–663, Figs. 15–21; Harvey 1991:320; Mahnert 2001:103; Harvey 2013:unpaginated.

Material examined.—None.

Diagnosis.—*Ideoroncus setosus* resembles *I. anophthalmus*, *I. cavicola*, *I. lenkoi*, *I. pallidus* and *I. paranensis* in having 20 trichobothria on the fixed chelal finger and hand, but has larger eyes, unlike *I. anophthalmus* and *I. cavicola*, which are eyeless, and *I. pallidus*, which has very small eyes, has a thickened subbasal band on the carapace not found in *I. paranensis*, and lower numbers of setae (9–11) on tergite IX found in *I. lenkoi*.

Description.—*Adult:* See Mahnert (1984a).

Nymphs: See Mahnert (1984a).

Remarks.—*Ideoroncus setosus* is recorded from São Paulo state, Brazil (Mahnert 1984a, 2001) (Fig. 26A).

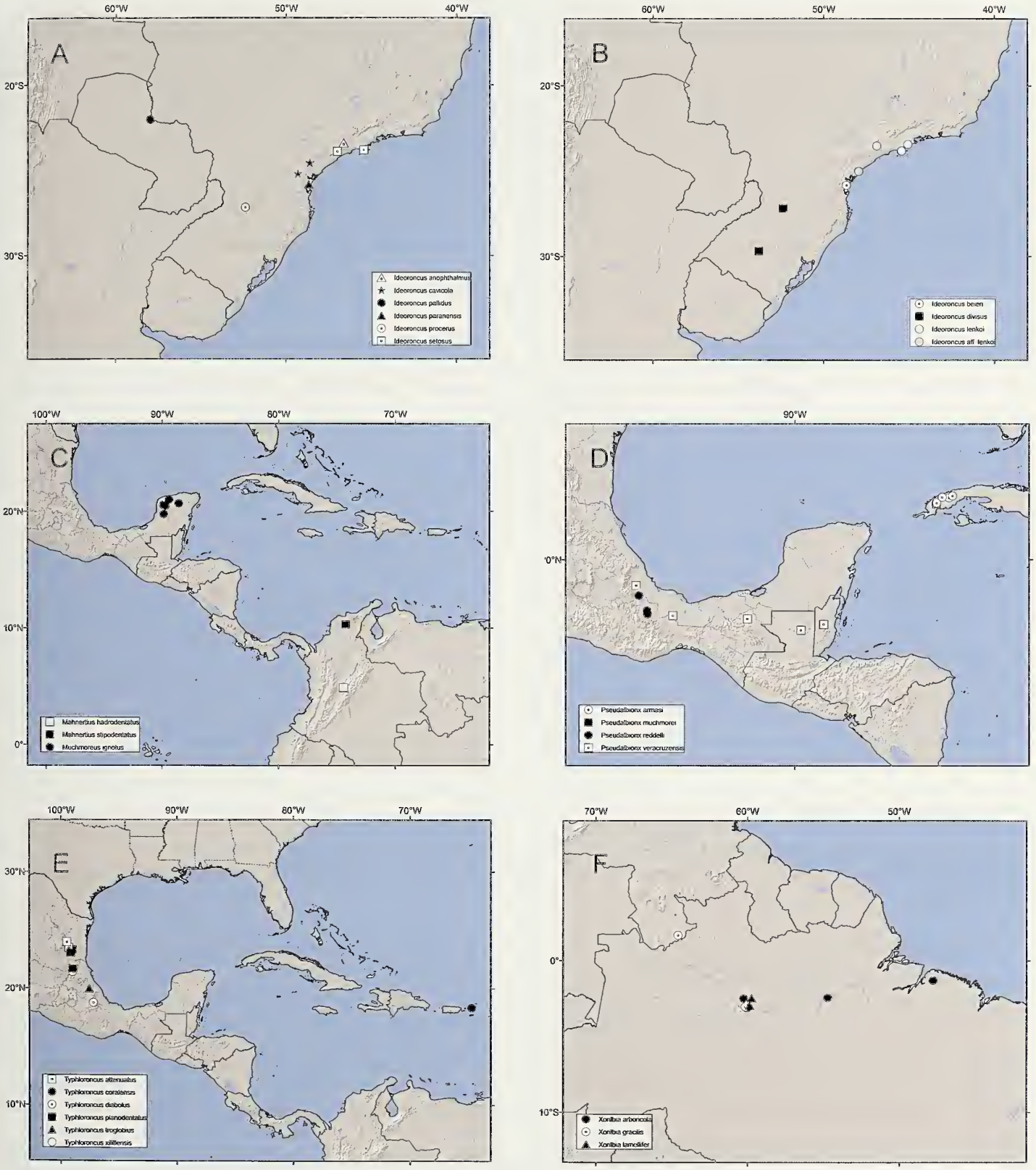

Figure 26.—Distribution of species of Ideoroncidae: A, B. *Ideoroncus* spp.; C. *Mahnertius* and *Muchmoreus*; D. *Pseudalbiorix* spp.; E. *Typhloroncus* spp.; F. *Xorilbia* spp.

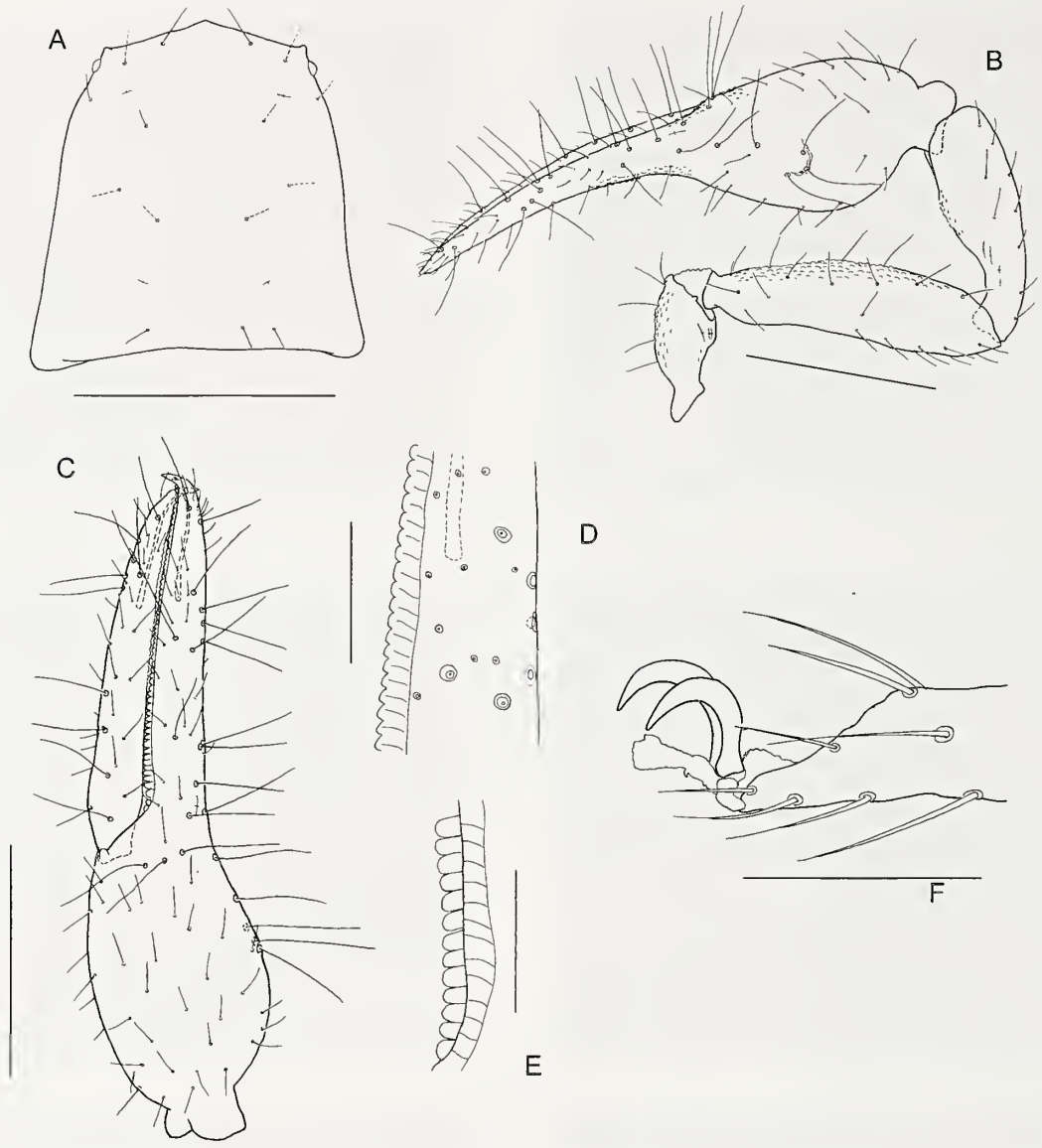

Figure 27.—*Mahnertius hadrodentatus* Harvey & Muchmore sp. nov., female holotype: A. Carapace, dorsal; B. Right pedipalp, dorsal; C. Left chela, lateral; D. fixed chelal finger, lateral; E. fixed chelal finger, basal region, lateral; F. Tip of right tarsus IV. Scale lines = 0.5 mm (A–C); 0.1 mm (D–F).

Genus ***Mahnertius*** Harvey & Muchmore gen. nov.

Type species.—*Mahnertius stipodentatus* Harvey & Muchmore sp. nov.

Diagnosis.—*Mahnertius* differs from all other ideoroncid genera in having the distal teeth of the fixed chelal finger compressed and enlarged (Figs. 28G, 28H). *Mahnertius* resembles species of *Xorilbia* and *Typhloroncus* in having arolia that are shorter than the claws (Figs. 27F, 28D) and that have a ventral hooked process, but the anal operculum does not closely abut sternite X as in *Typhloroncus*, and the arolia are not divided as in *Xorilbia*.

Description.—*Adult:* setae: long, straight and acicular.

Chelicera (Fig. 28B): hand with 6 setae; movable finger with 1 long subdistal seta; rallum of 4 thickened blades, all blades serrate (Fig. 28A); lamina exterior absent; galea long and slender.

Pedipalp (Figs. 27B, 28C): long and slender. Patella with disto-prolateral excavation. Fixed chelal finger and hand with 22 trichobothria, movable chelal finger with 10 trichobothria: *eb* region with 1 trichobothrium; *est* region with 6 trichobothria; *ib* region with 5 trichobothria; *ist* region with 6 trichobothria; *b* region with 2 trichobothria; *sb* and *st* regions with 1 trichobothrium; and *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *st* not ventrally displaced (Figs. 27C, 28E). Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus near *est* region in fixed finger and near *t* region in movable finger. Chelal teeth small and evenly spaced; distal teeth of the fixed chelal finger compressed and enlarged (Figs. 28G, 28H); base of fixed chelal finger with several small denticles. Chelal hand with retrolateral condyle small and rounded.

Carapace (Fig. 27A): with 2 small bulging eyes; without furrows; anterior margin with 4 setae.

Coxal region: manducatory process with 2 long distal setae. Median maxillary lyrifissure present and sub-basally situated.

Legs: femur I and II without basal swelling; femora I and II with primary slit sensillum directed transversely; femur I much longer than patella I; suture line between femur IV and patella IV transverse; metatarsus shorter than tarsus; metatarsal pseudotactile seta sub-proximal; legs with subterminal tarsal setae with small ventral denticulation; arolium shorter than claws, not divided, with ventral hooked protuberance; without sub-ungual spine; claws slender and simple (Figs. 27F, 28D).

Abdomen: tergites and sternites undivided. Pleural membrane longitudinally striate. Each stigmatic sclerite with 1 seta; spiracles simple, with spiracular helix. Anterior margin of anal operculum not abutting posterior margin of sternite X.

Genitalia: male median genital sac not visible in material examined; female with large gonosac covered with scattered pores.

Nymphs: Unknown.

Remarks.—This genus is quite distinct from other ideoroncids, and readily recognized by the morphology of the distal teeth of the fixed chelal finger. It is known only from Colombia (Figs. 2B, 26C).

Etymology.—This genus is named for Volker Mahnert, the former Director of the Muséum d'histoire naturelle de la Ville de Genève, and internationally renowned pseudoscorpion authority in honor of his contributions to arachnology.

KEY TO SPECIES OF *MAHNERTIUS*

1. Basal teeth of fixed chelal finger enlarged (Fig. 27E) ..... *M. hadrodentatus*
   Basal teeth of fixed chelal finger not enlarged (Fig. 28E) ..... *M. stipodentatus*

Mahnertius hadrodentatus Harvey & Muchmore sp. nov.
Figs. 26C, 27

Material examined.—*Holotype.* COLOMBIA: *Departamento de Cundinamarca*: female, Finca Bella Vista, near Sasaima (4°54′N, 74°26′W), 4 June 1965, under plant cover in root-soil leaf mold (duff), P.R. Craig (CAS).

Diagnosis.—*Mahnertius hadrodentatus* differs from *M. stipodentatus* by having enlarged basal teeth of the fixed chelal finger (Fig. 27E).

Description.—*Adult:* Color: pedipalps, carapace and coxae deep yellow-brown; appendages and abdominal segments yellow-brown.

Setae: generally long, straight and acicular.

Chelicera: hand with 6 setae; movable finger with 1 submedial seta; galea very slender and elongate; fixed finger with 10 (female) teeth; movable finger with 7 (female) teeth; rallum of 4 long blades, each with (basal to distal) 5, 9, 10 and 13 serrations; lamina exterior absent.

Pedipalp (Fig. 27B): trochanter with granules on prolateral face; femur with large granules on prolateral face; patella with fine granules on prolateral face; chela with very small denticles on prolateral face at base of fingers, on retrolateral face at base of fingers; basal half movable finger with granules on retrolateral face; trochanter 2.37 (female), femur 3.91 (female), patella 2.97 (female), chela (with pedicel) 3.88 (female), chela (without pedicel) 3.70 (female), hand 1.44 (female) x longer than broad, movable finger 1.55 (female) x longer than hand (without pedicel). Fixed chelal finger and hand with 22 trichobothria, movable chelal finger with 10 trichobothria (Fig. 27C): *eb*, *esb* and *isb* in straight row at base of finger; *eb* region with 1 trichobothrium; *ib* region with 5 trichobothria; *ist* region with 6 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus near *est* region in fixed finger and near basal section of *t* region in movable finger. Chelal teeth generally small and juxtadentate (Fig. 27D): fixed finger with 63 (female) teeth, including the 9 distal-most teeth raised into crest, and the basal teeth enlarged (Fig. 27E); movable finger with ca. 16 (female) low teeth, followed by smaller raised mounds; base of fixed chelal finger with several small denticles.

Carapace (Fig. 27A): lateral margins evenly convex; 1.11 × longer than broad; with 2 small bulging eyes; anterior margin medially prominent; with 15 setae including 4 on anterior margin and 4 on posterior margin; without furrows.

Coxal region: manducatory process somewhat pointed, with 2 apical acuminate setae; chaetotaxy 2 + 5: 4: 4: 5: 6 (female).

Legs: femur + patella 2.97 (female) x longer than deep; subterminal tarsal setae with small ventral denticulation; arolium shorter than claws, not divided, with ventral hooked process (Fig. 27F).

Abdomen: tergites and sternites undivided and uniseriate. Tergal chaetotaxy: female, 4: 4: 7: 10: 11: 11: 11: 12: 13: 11: 7 (including 4 tactile setae): 2. Sternal chaetotaxy: female, 6: (1) 4 (1): (1) 6 (1): 11: 13: 12: 11: 14: 11: 7 (including 4 tactile setae): 2. Setae of tergites and sternites IX–XI acuminate.

Genitalia: female with large gonosac which is covered with scattered pores.

Dimensions (mm): Female holotype: Body length ca. 2.4. Pedipalp: trochanter 0.425/0.179, femur 0.911/0.233, patella 0.698/0.235, chela (with pedicel) 1.670/0.430, chela (without pedicel) 1.590, hand (without pedicel) length 0.620, movable finger length 0.962. Chelicera 0.428/0.207, movable finger length 0.240. Carapace 0.740/0.666; eye diameter 0.045. Leg I: femur 0.485/0.121, patella 0.286/0.110, tibia 0.318/0.080, metatarsus 0.186/0.069, tarsus 0.317/0.052. Leg IV: femur + patella 0.760/0.256, tibia 0.533/0.118, metatarsus 0.266/0.095, tarsus 0.441/0.065.

Remarks.—*Mahnertius hadrodentatus* occurs in central Colombia (Fig. 26C).

Etymology.—The specific epithet refers to the large basal teeth of the fixed chelal finger, *hadros*, Greek, well-developed, bulky, and *dentatus*, Latin, toothed, pointed (Brown 1956).

Mahnertius stipodentatus Harvey & Muchmore sp. nov.
Figs. 25C, 28

Material examined.—*Holotype.* COLOMBIA: *Departamento del Magdalena*: male, San Pedro–San Javier, S.N. de Santa Marta (10°18′N, 74°14′W), 5,130 feet [= 1,563 m], 29 March 1975, leaf litter under rock, J.A. Kochalka (FSCA, WM4847.01001).

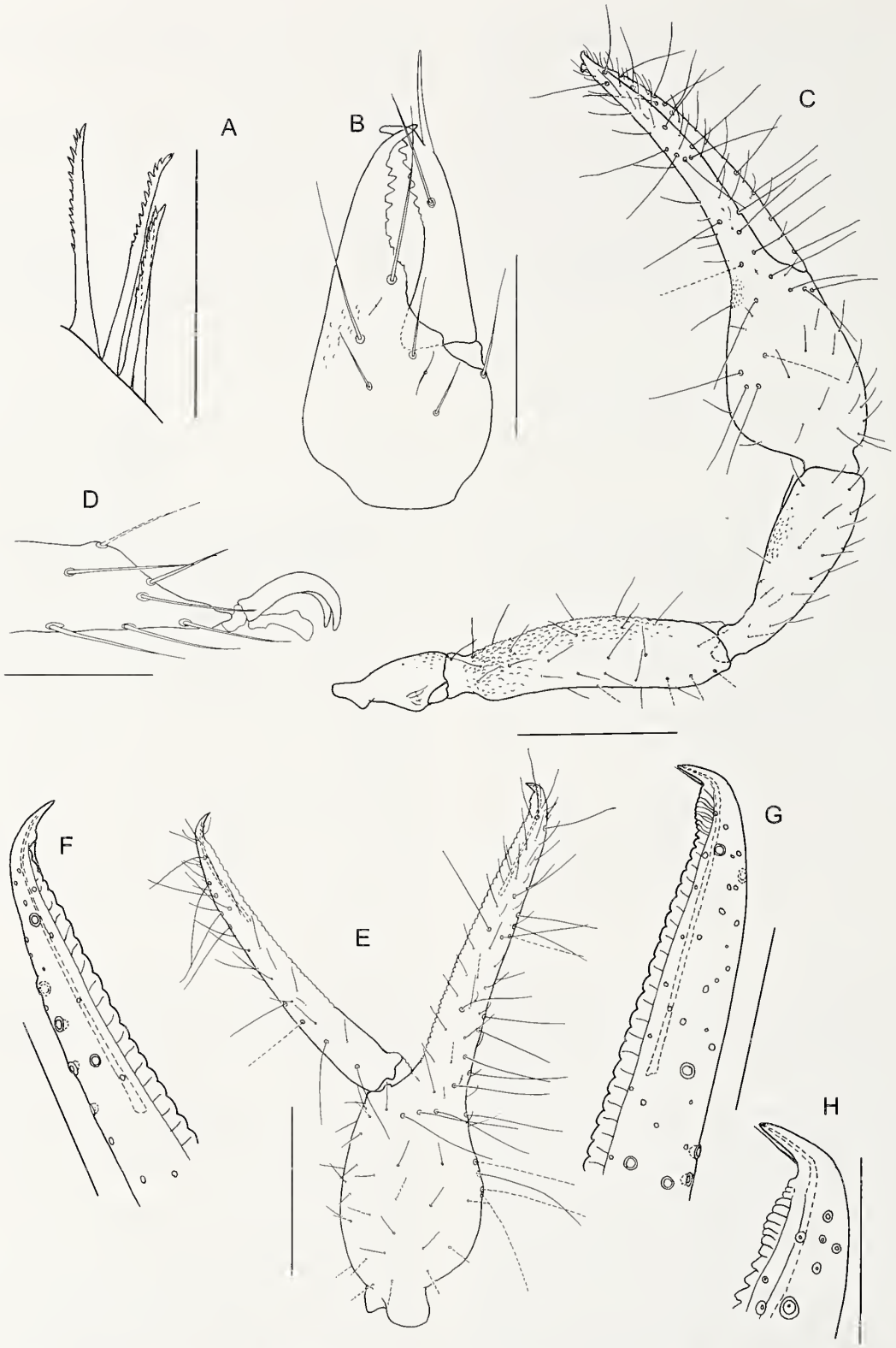

Figure 28.—*Mahnertius stipodentatus* Harvey & Muchmore sp. nov., male holotype: A. Left rallum; B. Right chelicera; C. Right pedipalp, dorsal; D. Tip of left tarsus IV; E. Left chela, lateral; F. movable chelal finger, lateral; G. fixed chelal finger, lateral; H. Tip of fixed chelal finger, lateral. Scale lines = 0.5 mm (C, E); 0.2 mm (B, F, G); 0.1 mm (A, D, H).

Paratype. COLOMBIA: *Departamento del Magdalena*: 1 female, collected with holotype (FSCA, WM4847.01002).

Diagnosis.—*Mahnertius stipodentatus* differs from *M. hadrodentatus* by not having the enlarged basal teeth of the fixed chelal finger (Fig. 28E) found in *M. hadrodentatus*.

Description.—*Adult:* Color: pedipalps, carapace and coxae deep yellow-brown; appendages and abdominal segments yellow-brown.

Setae: generally long, straight and acicular.

Chelicera: hand with 6 setae; movable finger with 1 submedial seta; galea very slender and elongate; fixed finger with 10 (male, female) teeth; movable finger with 7 (male, female) teeth; rallum of 4 long blades, each with 9–11 small serrations; lamina exterior absent.

Pedipalp (Fig. 28C): trochanter with granules on prolateral face; femur with large granules on prolateral face and basal half; patella with fine granules on prolateral face; chela with very small denticles on prolateral face at base of fingers; trochanter 2.45 (male), 2.52 (female), femur 4.06 (male), 3.96 (female), patella 3.17 (male), 2.83 (female), chela (with pedicel) 3.72 (male), 3.78 (female), chela (without pedicel) 3.54 (male), 3.58 (female), hand 1.32 (male), 1.40 (female) x longer than broad, movable finger 1.69 (male), 1.50 (female) x longer than hand (without pedicel). Fixed chelal finger and hand with 22 trichobothria, movable chelal finger with 10 trichobothria (Fig. 28E): *eb*, *esb* and *isb* in straight row at base of finger; *eb* region with 1 trichobothrium; *ib* region with 5 trichobothria; *ist* region with 6 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus near *est* region in fixed finger and near basal section of *t* region in movable finger. Chelal teeth generally small and juxtadentate: fixed finger with 58 (male), 59 (female) teeth, including the 8–9 distal-most teeth raised into crest (Figs. 28G, 28H); movable finger with 34 (male), 38 (female) low teeth (Fig. 28F); base of fixed chelal finger with several small denticles.

Carapace: lateral margins evenly convex; ? (damaged) x longer than broad; with 2 small bulging eyes; anterior margin medially prominent; with 18 setae including 4 on anterior margin and 4 on posterior margin; without furrows.

Coxal region: manducatory process somewhat pointed, with 2 apical acuminate setae; chaetotaxy 2 + 4: 4: 5: 3: 7 (♂); 2 + 4: 3: 5: 5: 5 (female).

Legs: femur + patella 2.67 (male), 3.00 (female) x longer than deep; subterminal tarsal setae with small ventral denticulation; arolium shorter than claws, not divided, with ventral hooked process (Fig. 28D).

Abdomen: tergites and sternites undivided and uniseriate. Tergal chaetotaxy: male, 4: 4: 6: 7: 9: 11: 12: 13: 12: 15: 12: 2; female, 4: 4: 4: 7: 9: 10: 11: 11: 13: 10 (including 2 tactile setae): 7 (including 4 tactile setae): 2. Sternal chaetotaxy: male, 7: (1) 12 [3 + 3] (1): (1) 6 (1): 11: 10: 12: 14: 15: 13: 5 (including 4 tactile setae): 2; female, 6: (1) 4 (1): (1) 6 (1): 10: 9: 13: 13: 13: 12: 7 (including 4 tactile setae): 2. Setae of tergites and sternites IX–XI aeuminate.

Genitalia: male with small dorsal apodeme; median genital sac not visible in material examined; female with large gonosac which is covered with scattered pores.

Dimensions (mm): Male holotype: Body length ca. 2.6. Pedipalp: trochanter 0.427/0.174, femur 0.898/0.221, patella 0.732/0.231, chela (with pedicel) 1.597/0.429, chela (without pedicel) 1.520, hand (without pedicel) length 0.568, movable finger length 0.958. Chelicera 0.414/0.201, movable finger length 0.243. Carapace ca. 0.68/? (crushed); eye diameter 0.048. Leg I: femur 0.467/0.122, patella 0.274/0.118, tibia 0.326/0.083, metatarsus 0.190/0.069, tarsus 0.321/0.058. Leg IV: femur + patella 0.768/0.288, tibia 0.539/0.128, metatarsus 0.282/0.103, tarsus 0.458/0.074.

Female paratype: Body length ca. 3.1. Pedipalp: trochanter 0.453/0.180, femur 0.914/0.231, patella 0.674/0.238, chela (with pedicel) 1.698/0.449, chela (without pedicel) 1.608, hand (without pedicel) length 0.630, movable finger length 0.947. Chelicera 0.458/0.219, movable finger length 0.277. Carapace ca. 0.67/? (crushed); eye diameter 0.051. Leg I: femur 0.484/0.127, patella 0.283/0.120, tibia 0.192/0.085, metatarsus 0.186/0.073, tarsus 0.307/0.058. Leg IV: femur + patella 0.789/0.263, tibia 0.594/0.123, metatarsus 0.291/0.106, tarsus 0.446/0.076.

Remarks.—*Mahnertius stipodentatus* occurs in northern Colombia (Fig. 26C).

Etymology.—The specific epithet refers to the compressed distal teeth of the fixed chelal finger, *stipo*, Latin, press, cram, crowd, and *dentatus*, Latin, toothed, pointed (Brown 1956).

Genus *Muchmoreus* Harvey gen. nov.

Type species.—*Muchmoreus ignotus* Harvey & Muchmore sp. nov.

Diagnosis.—*Muchmoreus* differs from all other ideoroncid genera by the position of trichobothrium *eb* which is situated slightly distal of *esb* (Fig. 29D), rather than on the same level as *esb*, and have 2 or 3 setae on the spiracular plates, whereas most other genera with the exception of *Pseudalbiorix* have a single seta. *Muchmoreus* resembles *Ideoroncus*, *Dhanus*, *Nhatrangia* and *Shravana* in having long, undivided arolia which lack a ventral hook (Fig. 29I). However, *Muchmoreus* lacks the medial suture line on the median sternites found in *Ideoroncus*, and lacks the cheliceral lamina exterior found in *Dhanus*, *Nhatrangia* and *Shravana*.

Description.—*Adult:* setae: long, straight and acicular.

Chelicera (Fig. 29B): hand with 6 or 7 setae; movable finger with 1 long subdistal seta; rallum of 4 thickened blades, all blades serrate; lamina exterior absent; galea long and slender.

Pedipalp (Fig. 29C): long and slender. Patella with large disto-prolateral excavation. Fixed chelal finger and hand with 20 trichobothria, movable chelal finger with 10 trichobothria (Fig. 29D): *eb* region with 1 trichobothrium; *eb* distal of *esb*; *est* region with 6 trichobothria; *ib* region with 4 trichobothria; *ist* region with 5 trichobothria; *b* region with 2 trichobothria; *sb* and *st* regions with 1 trichobothrium; and *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *st* not ventrally displaced. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus near *est* region in fixed finger and near *t* region in movable finger. Chelal teeth small and evenly spaced; base of fixed chelal finger with several small denticles. Chelal hand with retrolateral condyle small and rounded.

Carapace (Fig. 29A): with 2 large, bulging eyes; without furrows; anterior margin with 4 setae.

Coxal region: manducatory process with 2 long distal setae. Median maxillary lyrifissure present and sub-basally situated.

Legs: femur I and II without basal swelling; femora I and II with primary slit sensillum directed transversely; femur I much longer than patella I; suture line between femur IV and patella IV transverse; metatarsus shorter than tarsus; metatarsal pseudotactile seta sub-proximal; legs with trifurcate subterminal tarsal setae; arolium slightly longer than claws, not divided, without ventral hooked protuberance; without subungual spine; claws slender and simple (Fig. 29I).

Abdomen: tergites and sternites undivided. Pleural membrane longitudinally striate. Each stigmatic sclerite with 2 or 3 setae; spiracles simple, with spiracular helix. Anterior margin of anal operculum not abutting posterior margin of sternite X.

Genitalia: male median genital sac not visible in material examined; female with large gonosac covered with scattered pores.

Tritonymph. Fixed finger with 14 trichobothria, movable finger with 8 trichobothria (Fig. 29H); *ib* region with 3 trichobothria; *ist* region with 3 trichobothria; *est* region with 4 trichobothria; *et* slightly distal to *it*; *b* region with 1 trichobothrium; *t* region with 5 trichobothria; all other regions represented by 1 trichobothrium.

Remarks.—*Muchmoreus* is known only from the type species *M. ignotus* from Mexico (Figs. 2A, 26C).

Etymology.—This genus is dedicated to co-author William B. Muchmore in recognition of his contributions to systematic arachnology over a 40 year career. The name is to be treated as masculine.

Muchmoreus ignotus Harvey & Muchmore sp. nov.
Figs. 26C, 29

Material examined.—*Holotype.* MEXICO: *Yucatan*: male, 1 km S. of Muna (20°28′N, 89°43′W), 31 July–4 August 1973, J. Reddell (FSCA, WM3406.03001).

Paratypes. MEXICO: *Yucatan*: 3 female, same data as holotype (FSCA, WM3406.03002–4); 1 female, same data as holotype (WAM T129659, WM3406.03005); 1 male, Chichén Itzá (20°40′N, 88°34′W), under rocks, 8 August 1973, J. Reddell (FSCA, WM3402.02001); 1 male, same data (WAM T129660, WM3402.02002); 1 female, 3 km S. of Calcehtok (20°32′N, 89°54′W), under rocks, 3 August 1973, J. Reddell (FSCA, WM3404.01001); 1 male, 1 tritonymph, Tixkokob (21°00′N, 89°24′W), under rocks, 12 August 1973, J. Reddell (FSCA, WM3405.02001–2).

Other material. MEXICO: *Campeche*: 1 male, 2 km W. of Hopelchén (19°45′N, 89°52′W), 23 August 1972, Cooke, Russell, Mitchell (FSCA, WM3503.01001).

Diagnosis.—As for genus.

Description.—*Adult:* Color: pedipalps red-brown; carapace light red-brown; legs and abdomen pale yellow-brown.

Setae: generally long, straight and acicular.

Chelicera (Fig. 29B): hand with 6 setae, although the left chelicera of one female specimen bears 7 setae; movable finger with 1 subdistal seta; galea very slender and elongate; fixed finger with ca. 7 (male), 5 (female) small teeth; movable finger with ca. 4 (male), 5 (female) very small teeth; rallum of 4 blades, each with several small serrations; lamina exterior absent.

Pedipalp (Fig. 29C): femur and patella slightly rugose on interior face; trochanter 2.11–2.33 (male), 2.23–2.34 (female), femur 3.91–4.36 (male), 3.88–4.26 (female), patella 2.67–3.07 (male), 2.75–2.92 (female), chela (with pedicel) 3.72–4.08 (male), 3.46–3.84 (female), chela (without pedicel) 3.64–3.92 (male), 3.31–3.74 (female), hand (without pedicel) 1.36–1.56 (male), 1.35–1.48 (female) x longer than broad, movable finger 1.55–1.64 (male), 1.47–1.52 (female) x longer than hand (without pedicel). Fixed chelal finger and hand with 20 trichobothria, movable chelal finger with 10 trichobothria (Fig. 29D): *eb*, *esb* and *isb* at base of finger, *eb* situated slightly distal of *esb*; *eb* region with 1 trichobothrium; *ib* region with 4 trichobothria; *ist* region with 5 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus near *est* region in fixed finger and near basal section of *t* region in movable finger. Chelal hand with retrolateral condyle small and rounded. Chelal teeth small, evenly spaced, conical and slightly retrorse, movable finger with 2 enlarged teeth at distal end; fixed finger with ca. 46–56 (male), 42–52 (female) teeth; movable finger with ca. 36–39 (male), 33–37 (female) teeth; base of fixed chelal finger with several small denticles.

Carapace (Fig. 29A): lateral margins evenly convex; 1.11–1.45 (male), 1.13–1.36 (female) x longer than broad; with 2 large, bulging eyes; anterior margin medially prominent; with 20–22 (male), 20–21 (female) setae including 4 setae on anterior margin and 4, occasionally 5 or 6, on posterior margin; without furrows.

Coxal region: manducatory process somewhat pointed, with 2 apical acuminate setae; chaetotaxy 2 + 6: 4: 5–6: 6: 7–8 (male); 2 + 7: 4: 5–6: 6: 6–9 (female).

Legs: femur + patella 2.17–2.34 (male), 2.31–2.47 (female) x longer than deep; subterminal tarsal setae trifurcate; arolium slightly longer than claws, not divided, without ventral hooked process.

Abdomen: tergites and sternites not divided and uniseriate. Tergal chaetotaxy: male, 4: 4–7: 6–9: 8–9: 8–9: 7–9: 8–10: 8–10: 9–10: 7–10: 6: 2; female, 4–5: 4–6: 8–9: 8–9: 8–10: 8–9: 8–11: 8–10: 9–10: 8–10: 4–7: 2. Sternal chaetotaxy: male, 13–16: (2–3) 13–18 [3 + 3] (2–3): (2) 6–8 (2): 10–13: 10–12: 11–12: 11–12: 11: 10–12: 8: 2; female, 8–11: (2–3) 4–7 (2–3): (2–3) 6–7 (2–3): 10–13: 11–12: 11–13: 11–13: 11: 11–13: 8: 2. Setae of female sternite II reduced in size, but not minute, ca. 9–10 μm in length; setae of tergites and sternites IX–XI acuminate; with several tactile setae.

Genitalia: male with small dorsal apodeme; median genital sac not visible in material examined; female with large gonosac, which is covered with scattered pores.

Dimensions (mm): Male: holotype followed by other males (where applicable): Body length 2.58 (2.39–2.68). Pedipalp: trochanter 0.39/0.175 (0.38–0.40/0.165–0.19), femur 0.86/0.22 (0.85–0.87/0.195–0.21), patella 0.665/0.23 (0.64–0.66/0.215–0.24), chela (with pedicel) 1.45/0.39 (1.41–1.57/0.36–0.40), chela (without pedicel) length 1.42 (1.36–1.55), hand (without pedicel) length 0.53 (0.54–0.59), movable finger length 0.87 (0.835–0.910). Chelicera 0.32–0.155; movable finger length 0.19. Carapace 0.84/0.58 (0.80–0.84/0.63–0.72); eye diameter 0.065. Leg I: femur 0.41/0.105, patella 0.20/0.095, tibia 0.29/0.075, metatarsus 0.20/0.06, tarsus 0.28/0.05. Leg IV: femur + patella 0.72/0.325 (0.69–0.76/0.31–0.35, tibia 0.47/0.12, metatarsus 0.25/0.09, tarsus 0.35/0.06.

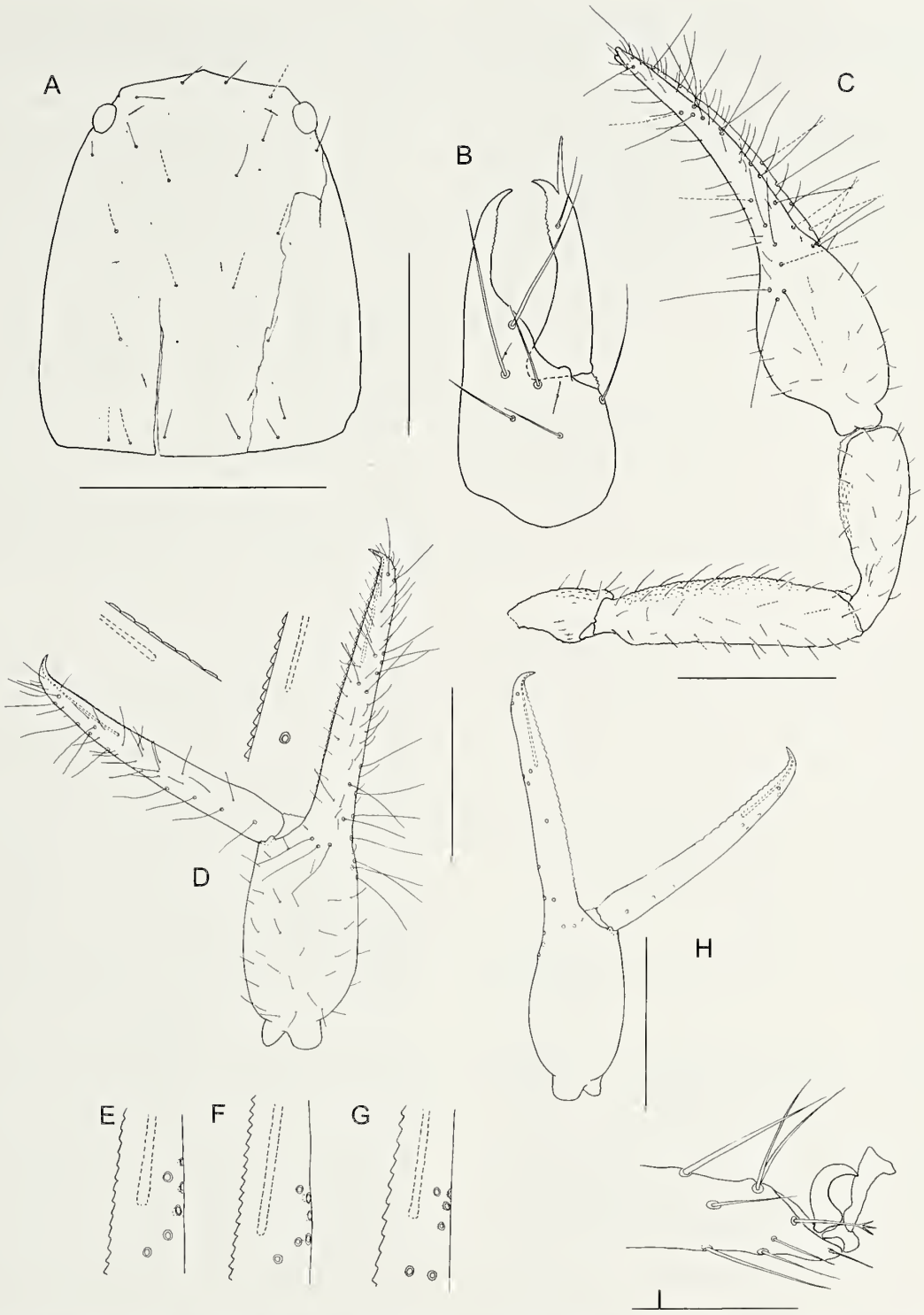

Figure 29.—*Muchmoreus ignotus* Harvey & Muchmore sp. nov., male holotype, unless stated otherwise: A. Carapace; B. Left chelicera, dorsal; C. Right pedipalp, dorsal; D. Left chela, lateral; E–G, teeth of the fixed chelal finger, showing variation in trichobothrial position: E (FSCA, WM 3405.02001), F (FSCA, WM 3402.02002), G (FSCA, WM 3402.02001); H. Right chela, setae omitted, lateral, tritonymph paratype (FSCA, WM 3405.02002); I. Tip of right tarsus IV. Scale lines = 0.5 mm (A, C, D, H); 0.2 mm (B); 0.1 mm (I).

Female (WM3406.03002), followed by other females (where applicable): Body length 3.00 (2.82–3.07). Pedipalp: trochanter 0.43/0.19 (0.445/0.19–0.20), femur 1.00/0.235 (0.96–0.97/0.235–0.25), patella 0.73/0.25 (0.70–0.74/0.245–0.26), chela (with pedicel) 1.71/0.445 (1.62–1.67/0.435–0.48), chela (without pedicel) length 1.665 (1.590–1.61), hand (without pedicel) length 0.66 (0.635–0.66), movable finger length 0.985 (0.95–0.97). Chelicera 0.38/0.17; movable finger length 0.22. Carapace 0.895/0.67 (0.850–0.925/0.680–0.815); eye diameter 0.064. Leg I: femur 0.465/0.125, patella 0.23/0.115, tibia 0.32/0.085, metatarsus 0.22/0.065, tarsus 0.31/0.05. Leg IV: femur + patella 0.805/0.34 (0.76–0.815/0.31–0.34, tibia 0.525/0.125, metatarsus 0.295/0.095, tarsus 0.39/0.065.

Tritonymph: Chelicera: galea long, nearly straight; hand with 5 setae, movable finger with 1 seta; fixed finger with 6 small teeth, movable finger with 5 small teeth; rallum composed of 4 blades, all serrate.

Pedipalp: trochanter 2.10, femur 3.89, patella 2.70, chela (with pedicel) 4.10, chela (without pedicel) 4.02 × longer than broad. Fixed finger with 14 trichobothria, movable finger with 8 trichobothria (Fig. 29H); *eb* region with 1 trichobothrium; *ib* region with 3 trichobothria; *ist* region with 3 trichobothria; *est* region with 4 trichobothria; *et* slightly distal to *it*; *b* region with 1 trichobothrium; *t* region with 5 trichobothria.

Carapace: 1.15 × longer than broad; anterior margin medially prominent; 1 pair of small eyes present; with 4 setae on anterior margin and 4 setae on posterior margin.

Legs: mostly as in adult.

Dimensions (mm): Body length 2.37. Pedipalp: trochanter 0.325/0.155, femur 0.70/0.18, patella 0.50/0.185, chela (with pedicel) 1.23/0.30, chela (without pedicel) 1.205, hand (without pedicel) length 0.46, movable finger length 0.74. Carapace 0.70/0.61.

Remarks.—*Muchmoreus ignotus* has been found under rocks in a variety of Mexican localities in Yucatan and in neighboring Campeche (Fig. 26C).

Etymology.—The Latin specific epithet *ignotus* (unknown, strange) refers to the necessity for us to erect a new genus to accommodate this species.

Genus *Pseudalbiorix* Harvey, Barba, Muchmore and Peréz 2007

Pseudalbiorix Harvey, Barba, Muchmore and Peréz 2007:611; Harvey 2013:unpaginated.

Type species.—*Albiorix reddelli* Muchmore 1982b, by original designation.

Diagnosis.—*Pseudalbiorix* differs from all other ideoroncids by the enlarged, bifurcate retrolateral chelal condyle (Harvey et al. 2007).

Description.—*Adult:* See Harvey et al. (2007). In addition: base of fixed chelal finger without small denticles.

Nymphs: See Harvey et al. (2007).

Remarks.—The four species of *Pseudalbiorix* are found in Central America and western Cuba (Harvey et al. 2007) (Figs. 2B, 26D).

KEY TO SPECIES OF *PSEUDALBIORIX* (FROM HARVEY ET AL. 2007)

1. Most teeth of fixed chelal finger long and erect, clearly longer than wide 2
   Most teeth of fixed chelal finger of medium length and retrorse, clearly wider than long 3
2. Large troglomorphic species, e.g., pedipalpal femur 1.26–1.39 mm in length; chela (without pedicel) 2.10–2.24 mm in length. . . . . *P. muchmorei*
   Medium-sized epigean species, e.g., pedipalpal femur 0.68–1.03 mm in length; chela (without pedicel) 1.14–1.68 mm in length. . . . . *P. armasi*
3. Slightly larger in size, e.g., chela (with pedicel) length greater than 1.20 mm; most teeth of fixed chelal finger triangular . . . *P. reddelli*
   Slightly smaller in size, e.g., chela (with pedicel) length less than 1.20 mm; most teeth of fixed chelal finger arcuate . . . . *P. veracruzensis*

Pseudalbiorix armasi Barba and Pérez 2007
Fig. 26D

Pseudalbiorix armasi Barba and Pérez, in Harvey, Barba, Muchmore and Pérez 2007:623–625, Figs. 2, 33–37; Harvey 2013:unpaginated.

Material examined.—See Harvey et al. (2007), as well as: CUBA: *Pinar del Rio:* 1 male, Los Banos de San Vincente (22°40′N, 83°43′W), 1 August (no year stated), Parsons (MCZ, Hoff slide S–3299).

Diagnosis.—Like *P. muchmorei*, this species has large, erect chelal teeth, but differs by being smaller, e.g., pedipalpal femur 0.68–1.03 mm in length, and chela (without pedicel) 1.14–1.68 mm in length.

Description.—*Adult:* See Harvey et al. (2007).

Nymphs: See Harvey et al. (2007).

Remarks.—*Pseudalbiorix armasi* is known only from Pinar del Río Province, Cuba (Fig. 26D).

Pseudalbiorix muchmorei Barba and Pérez 2007
Fig. 26D

Pseudalbiorix muchmorei Barba and Pérez, in Harvey, Barba, Muchmore and Pérez 2007:621–623, Figs. 3, 28–32; Harvey 2013:unpaginated.

Material examined.—See Harvey et al. (2007).

Diagnosis.—Like *P. armasi*, this species has large, erect chelal teeth, but differs by being larger, e.g., pedipalpal femur 1.26–1.39 mm in length, and chela (without pedicel) 2.10–2.24 mm in length.

Description.—*Adult:* See Harvey et al. (2007).

Remarks.—*Pseudalbiorix muchmorei* is known only from caves situated in Pinar del Río Province, Cuba (Fig. 26D).

Pseudalbiorix reddelli (Muchmore 1982)
Fig. 26D

Albiorix reddelli Muchmore 1982b:77, Figs. 37–40; Mahnert 1984a:676–677, Fig. 47 [as *Albiorix* (?) *reddeli* (sic)]; Harvey 1991:318; Ceballos 2004:428.

Pseudalbiorix reddelli (Muchmore): Harvey et al. 2007:613–618, Figs. 1, 2, 8–22; Harvey & Volschenk 2007:368, Figs. 1–4; Harvey 2013:unpaginated.

Material examined.—See Harvey et al. (2007).

Diagnosis.—Like *P. veracruzensis*, this species has medium length chelal teeth, but differs by being slightly larger, e.g. chela (with pedicel) length greater than 1.20 mm, and most teeth of fixed chelal finger triangular.

Description.—*Adult:* See Harvey et al. (2007).

Nymphs: See Harvey et al. (2007).

Remarks.—This species was originally described from specimens collected within Grutas de Monteflor, Oaxaea, Mexico (Muchmore 1982b) and was redescribed from numerous specimens by Harvey et al. (2007). It is only known from southern Mexico (Fig. 26D).

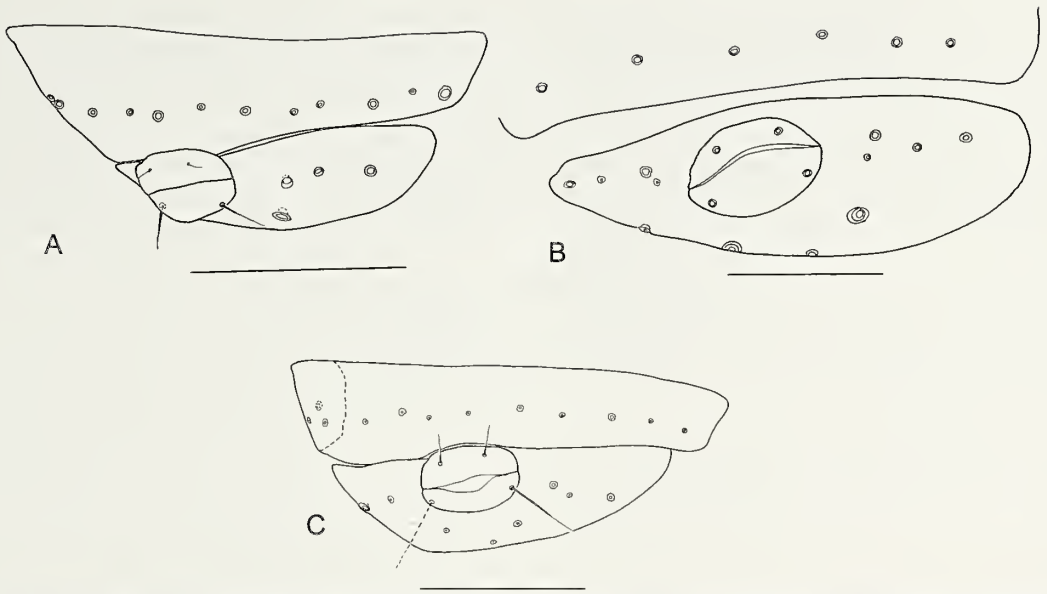

Figure 30.—*Typhloroncus* spp., anal region, ventral: A. *T. coralensis* Muchmore (distorted during slide preparation), male (FSCA, WM6566.02001); B. *T. xilitlensis* Muchmore, male holotype (FSCA, WM6104.01001); C. Anal region, ventral. Scale lines = 0.2 mm.

Pseudalbiorix veracruzensis (Hoff 1945)
Figs. 1A, 1B, 26D

Albiorix veracruzensis Hoff 1945:4–7, figs 6–9; Harvey 1991:318; Ceballos 2004:428.

Pseudalbiorix veracruzensis (Hoff): Harvey et al. 2007:619–621, Figs. 3, 8, 23–27; Murienne et al. 2008:174; Harvey 2013:unpaginated.

Material examined.—See Harvey et al. (2007).

Diagnosis.—Like *P. reddelli*, this species has medium length chelal teeth, but differs by being slightly smaller, e.g., chela (with pedicel) length less than 1.20 mm, and most teeth of fixed chelal finger arcuate.

Description.—*Adult:* See Harvey et al. (2007).

Nymphs: See Harvey et al. (2007).

Remarks.—Originally described in the genus *Albiorix*, this species was transferred to the genus *Pseudalbiorix* by Harvey et al. (2007). It is known from various locations in Belize, Guatemala and southern Mexico (Fig. 26D).

Genus *Typhloroncus* Muchmore 1979

Typhloroncus Muchmore 1979:317–318; Mahnert 1984a:677; Muchmore 1986:27–28; Harvey 1991:322; Harvey 2013:unpaginated.

Type species.—*Typhloroncus coralensis* Muchmore 1979, by original designation.

Diagnosis.—*Typhloroncus* can be distinguished from all other ideoroncid genera by the position of the anal operculum which either abuts sternite X or is situated very close to it (Figs. 30A–C).

Description.—*Adult:* setae: long, straight and acicular.

Chelicera: hand with 5 or 6 setae; movable finger with 1 long subdistal seta; rallum of 4 blades, all blades serrate; lamina exterior absent; galea long and slender.

Pedipalp (Fig. 31C): long and slender. Patella with disto-prolateral excavation. Fixed chelal finger and hand with 22 trichobothria, movable chelal finger with 10 trichobothria (Fig. 31E): *eb* region with 1 trichobothrium; *est* region with 6 trichobothria; *ib* region with 4 trichobothria; *ist* region with 6 trichobothria; *b* region with 2 trichobothria; *sb* and *st* regions with 1 trichobothrium; and *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus near *est* region in fixed finger and near *t* region in movable finger. Chelal teeth all closely spaced (Figs. 31F, 31G); base of fixed chelal finger with several small denticles. Chelal hand with retrolateral condyle small and rounded.

Carapace: eyes present (Figs. 31A, 31B) or absent; with or without posterior furrow; anterior margin with 4 or occasionally 5 setae.

Coxal region: manducatory process with 2 long distal setae. Median maxillary lyrifissure present and sub-basally situated.

Legs: femur I and II without basal swelling; femora I and II with primary slit sensillum directed transversely; femur I much longer than patella I; suture line between femur IV and patella IV transverse; metatarsus shorter than tarsus; metatarsal pseudotactile seta sub-proximal; legs with subterminal tarsal setae terminally denticulate, acicular or strongly lanceolate; arolium shorter than claws, not divided, with ventral hooked protuberance; without sub-ungual spine; claws slender and simple (Fig. 31D).

Abdomen: tergites and sternites undivided, medial sternites without medial suture line. Pleural membrane longitudinally striate. Each stigmatic sclerite with 1 seta; spiracles simple, with spiracular helix. Anterior margin of anal operculum touching posterior margin of sternite XI (Figs. 30A–C).

Genitalia: male median genital sac bipartite; female with large gonosac covered with scattered pores.

Nymphs: Unknown.

Remarks.—The genus *Typhloroncus* was proposed by Muchmore (1979) for a small blind ideoroncid from the U.S. Virgin Islands and was later extended with the description of

four large troglobites from Mexico (Muchmore 1982b, 1986) (Figs. 2B, 26E). Members of the genus are currently characterised by the lack of eyes, the short, undivided arolium, the number of trichobothria, and the presence of a dorsal eminence on the chelal hand (Muchmore 1982b). Most notably they lack various features diagnostic of other genera, such as the divided arolium in *Albiorix*, the bipartite retrolateral chelal condyle in *Pseudalbiorix*, and the widely spaced teeth of *Xorilbia*. We have found during this study that the anal operculum closely abuts the posterior margin of sternite X in all five named species of *Typhloroncus*, as well as in the new epigean species from Mexico (Figs. 30A–C). The discovery of an eyed species of *Typhloroncus* necessitates a modification of the genus, which we propose can be diagnosed by the juxtaposition of the anal operculum and sternite X. This peculiar morphology is not found in any other ideoroncid genus.

KEY TO SPECIES OF *TYPHLORONCUS*

1. Smaller, epigean species, e.g., pedipalpal femur less than 1 mm in length 2
   Larger, troglobitic species, e.g., pedipalpal femur greater than 2 mm in length 3
2. Eyes present (Figs. 31A, 31B) . . . . . *T. plauodentatus*
   Eyes absent . . . . . *T. coralensis*
3. Ventral and subterminal tarsal setae of all legs strongly lanceolate . . . . . *T. attenuatus*
   Ventral and subterminal tarsal setae of legs unmodified 4
4. Pedipalpal segments slender, e.g., femur of female 4.5 × longer than broad; chela (without pedicel) of female 4.5 × longer than broad . . . . . *T. diabolus*
   Pedipalpal segments very slender, e.g., femur of female greater than 7.0 × longer than broad; chela (without pedicel) of female greater than 5.5 × longer than broad 5
5. Pedipalpal femur of female 2.03 mm long and 7.25 × longer than broad; chela (without pedicel) of female 3.11 mm long and 5.9 × longer than broad . . . . . *T. troglobius*
   Pedipalpal femur of female 2.37 mm long and 7.65 × longer than broad; chela (without pedicel) of female 3.77 mm long and 6.85 × longer than broad . . . . . *T. xilitlensis*

Typhloroncus attenuatus Muchmore 1982
Fig. 26E

Typhloroncus attenuatus Muchmore 1982b:73–75, Figs. 30–32; Mahnert 1984a:677–678, Fig. 50; Muchmore 1986:28; Harvey 1991:322; Ceballos 2004:428; Villegas-Guzmán 2009:64–66, Figs. 1–7; Harvey 2013:unpaginated.

Material examined.—*Holotype.* MEXICO: *Tamaulipas*: female, Cueva del Brinco, near Conrado Castillo, about 40 km NW. of Ciudad Victoria (23°29′N, 99°19′W), April 1978, A. Grubbs, D. Pate, P. Sprouse, T. Treacy, S. Balsdon, R. Hemperly, P. Strickland (FSCA, WM5465.01001).

Diagnosis.—*Typhloroncus attenuatus* is a large blind troglobite that differs from all other species of the genus by the strongly lanceolate subterminal and ventral tarsal setae of all legs.

Description.—*Adult:* See Muchmore (1982b, 1986) and Villegas-Guzmán & Francke (2009) (but see Remarks below).

Remarks.—The original description was based on a single female from Cueva del Brinco, Tamaulipas, Mexico (Muchmore 1982b), and later augmented by the description of two males from Sistema Cavernario Purificación (Villegas-Guzmán & Francke 2009), which is situated some 60 km to the north of the type locality (Fig. 26E).

Villegas-Guzmán & Francke (2009) claimed that the carapace of their male bore 60 setae but this is likely to be an overestimate, as the holotype only bears 11 setae Muchmore (1982b). The discrepancy has probably arisen by mistaking the many small euticular pores on the carapace with setal areoles.

Typhloroncus coraleusis Muchmore 1979
Fig. 26E

Typhloroncus coralensis Muchmore 1979: 318–319, Figs. 1–5; Muchmore 1982b:71; Mahnert 1984a:677, Fig. 48; Muchmore 1986:28, Fig. 19; Harvey 1991:322; Muchmore 1993:32; Harvey et al. 2007:Fig. 7; Harvey 2013:unpaginated.

Material examined.—US VIRGIN ISLANDS: *Saint John*: 1 male, above Coral Bay, Saint John Island (18°21′N, 64°43′W), 9 May 1984, under rock, W.B. Muchmore (FSCA, WM6566.02001).

Diagnosis.—*Typhloroncus coralensis* is the only epigean species of the genus that eompletely lacks eyes.

Description.—*Adult male:* Color: pedipalps red-brown; carapace light red-brown; legs and abdomen pale yellow-brown.

Setae: generally long, straight and acicular.

Chelicera: hand with 6 setae; movable finger with 1 submedial seta; galea very slender and elongate; fixed finger with 16 small teeth; movable finger with 7 small teeth; rallum of 4 blades, each with several serrations; lamina exterior absent.

Pedipalp: Mostly smooth except for most of trochanter, the prolateral faces of the femur, patella and chela, and the retrolateral face of the chelal fingers which are lightly tuberculate; trochanter 2.50, femur 4.24, patella 3.50, chela (with pedicel) 3.88, chela (without pedicel) 3.65, hand 1.49 × longer than broad, movable finger 1.48 × longer than hand (without pedicel). Fixed chelal finger and hand with 22 trichobothria, movable chelal finger with 10 trichobothria: *eb*, *esb* and *isb* in straight row at base of finger; *eb* region with 1 trichobothrium; *ib* region with 5 trichobothria; *ist* region with 6 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus slightly distal to *est* region in fixed finger and within *t* region in movable finger. Chelal teeth: fixed finger with 66 low, juxtadentate teeth; movable finger with ca. 24 low, juxtadentate teeth; base of fixed chelal finger with several small denticles.

Carapace: lateral margins evenly convex; ? x longer than broad (flattened); eyes absent; anterior margin medially prominent; with 18 setae including 4 on anterior margin and 4 on posterior margin; with obvious posterior furrow.

Coxal region: manducatory process somewhat pointed, with 2 apical acuminate setae; chaetotaxy: 2 + 7: 4: 6: 7: 6.

Legs: femur + patella 2.36 × longer than deep; subterminal tarsal setae terminally denticulate; arolium about as long as claws, not divided, with ventral hooked process.

Abdomen: tergites and sternites not divided and uniseriate. Tergal chaetotaxy: 4: 4: 6: 9: 7: 7: 9: 9: 9: 9: 6 (including 4 tactile setae): 2. Sternal chaetotaxy: 8: (1) 9 [3 + 4] (1): (1) 6 (1): 8: 8: 9: 10: 9: 12: 6 (including 4 tactile setae): 2. Setae of tergites and sternites IX–XI acuminate. Anterior margin of anal operculum touching posterior margin of sternite XI.

Genitalia: male median genital sac not visible in material examined.

Dimensions (mm): Body length ca. 2.0. Pedipalp: trochanter 0.351/0.137, femur 0.704/0.166, patella 0.584/0.167, chela (with pedicel) 1.182/0.305, chela (without pedicel) 1.112, hand (without pedicel) length 0.454, movable finger length 0.672. Chelicera 0.321/0.154, movable finger length 0.186. Carapace 0.570/? (flattened). Leg I: femur 0.316/0.086, patella 0.174/0.084, tibia 0.269/0.058, metatarsus 0.122/0.045, tarsus 0.231/0.038. Leg IV: femur + patella 0.487/0.206, tibia 0.372/0.091, metatarsus 0.180/0.059, tarsus 0.282/0.042.

Remarks.—*Typhloroncus coralensis* is found in the US Virgin Islands where it occurs under rocks on wooded hillsides (Muchmore 1979) (Fig. 26E). Mahnert (1984a) and Muchmore (1986) provided illustrations of the chelal trichobothrial pattern. The original description of the adult female is here supplemented with the description of an adult male from the type locality.

Typhloroncus diabolus Muchmore 1982
Fig. 26E

Typhloroncus diabolus Muchmore 1982b:73, Figs. 27–29; Mahnert 1984a:677, Fig. 51; Muchmore 1986:28; Harvey 1991:322; Ceballos 2004:428; Harvey 2013:unpaginated.

Material examined.—*Holotype.* MEXICO: *Veracruz*: female, Cueva del Diablo, 3 km SSW. of Ciudad Mendoza (18°47′N, 97°11′W), 7 March 1973, J.R. Reddell, S. Murphy (FSCA, WM3415.01001).

Diagnosis.—*Typhloroncus diabolus* is a large, blind troglobite that differs from *T. attenuatus* by the lack of lanceolate setae on the leg tarsi, and from *T. troglobius* and *T. xilitlensis* by the less slender pedipalpal segments, e.g., femur of female 4.5 × longer than broad, and chela (without pedicel) of female 4.5 × longer than broad.

Description.—*Adult:* See Muchmore (1982b) and (Mahnert 1984a).

Remarks.—*Typhloroncus diabolus* was described by Muchmore (1982b) from a single female from Cueva del Diablo, Mexico (Fig. 26E). Mahnert (1984a) provides an illustration of the chelal trichobothrial pattern.

Typhloroncus planodentatus Harvey & Muchmore sp. nov.
Figs. 26E, 31

Material examined.—*Holotype.* MEXICO: *San Luis Potosí*: male, 20 miles S. of Vallea (most likely Ciudad Valles; see Remarks) (21°41′N, 98°58′W), 14 April 1946 [L.I.] Davis (AMNH, Hoff slide S–1194).

Paratype. MEXICO: *Tamaulipas*: 1 female, Gomez Farias (23°03′N, 99°09′W), 15 February 1970, J.A.L. Cooke (FSCA, WM2103.01001).

Other material. MEXICO: *Tamaulipas*: 1 male, Mesa Llera (23°19′N, 99°01′W), 16 May 1974, epigean, Elliott *et al.* (FSCA, WM3872.01001).

Diagnosis.—*Typhloroncus planodentatus* is the only known species of the genus that possesses eyes (Figs. 31A, 31B).

Description.—*Adult:* Color: pedipalps red-brown; carapace light red-brown; legs and abdomen pale yellow-brown.

Setae: generally long, straight and acicular.

Chelicera: hand with 6 (occasionally 7) setae; movable finger with 1 submedial seta; galea very slender and elongate; fixed finger with 7 (male), 7 (female) small teeth; movable finger with 8 (male), 8 (female) small teeth; rallum of 4 blades, each with small serrations; lamina exterior absent.

Pedipalp (Fig. 31C). Mostly smooth except for retrolateral face of trochanter, and the prolateral faces of the femur, patella and chela, which are lightly tuberculate; trochanter 2.45–2.64 (male), 2.33 (female), femur 3.58–4.57 (male), 3.70 (femle), patella 2.84–3.47 (male), 2.78 (female), chela (with pedicel) 3.46–4.06 (male), 3.13 (female), chela (without pedicel) 3.27–3.81 (male), 2.94 (female), hand 1.32–1.52 (male), 1.25 (female) x longer than broad, movable finger 1.54–1.57 (male), 1.38 (female) x longer than hand (without pedicel). Fixed chelal finger and hand with 22 trichobothria, movable chelal finger with 10 trichobothria (Fig. 31E): *eb*, *esb* and *isb* in straight row at base of finger; *eb* region with 1 trichobothrium; *ib* region with 5 trichobothria; *ist* region with 6 trichobothria; *est* region with 6 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *t* region with 6 trichobothria; *sb* not dorsally displaced relative to *st*; *t* region not overlapping with *est* region. Venom apparatus present in both chelal fingers, venom duct terminating in nodus ramosus slightly distal to *est* region in fixed finger and within *t* region in movable finger. Chelal teeth: fixed finger with 54–55 (male), 48 (female) teeth, truncate and flat-topped, becoming slightly angulate in basal half of finger (Fig. 31G); movable finger with ca. 45–48 (male), 40 (female) teeth, truncate and flat-topped (Fig. 31F); base of fixed chelal finger with several small denticles.

Carapace (Fig. 31A): lateral margins evenly convex; 1.34 (male) x longer than broad (female distorted); with 2 small bulging eyes; with anterior margin medially prominent; with 18 setae including 4 on anterior margin and 4 on posterior margin; without furrows.

Coxal region: manducatory process somewhat pointed, with 2 apical acuminate setae; chaetotaxy: 2 + 5: 4: 5: 5: 5 (male); 2 + 6: 5–6: 4: 5: 6 (female).

Legs: femur + patella 2.21–2.33 (male), 2.42 (female) x longer than deep; subterminal tarsal setae acuminate, without additional rami (Fig. 31D); arolium slightly shorter than claws, not divided, with ventral hooked process (Fig. 31D).

Abdomen: tergites and sternites not divided and uniseriate. Tergal chaetotaxy: male, 4: 4: 8: 8: 8: 8: 8: 10: 10: 10: 6 (including 4 tactile setae): 2; female, 4: 5: 8: 8: 8: 8: 9: 9: 10: 5 (including 4 tactile setae): 2. Sternal chaetotaxy: male, 7: (1) 8 [3 + 3] (1): (1) 4 (1): 8: 8: 10: 10: 11: 10: 4 (including 2 tactile setae): 2; female, 7: (1) 6 (1): (1) 5 (1): 8: 8: 8: 9: 11: 10: 4

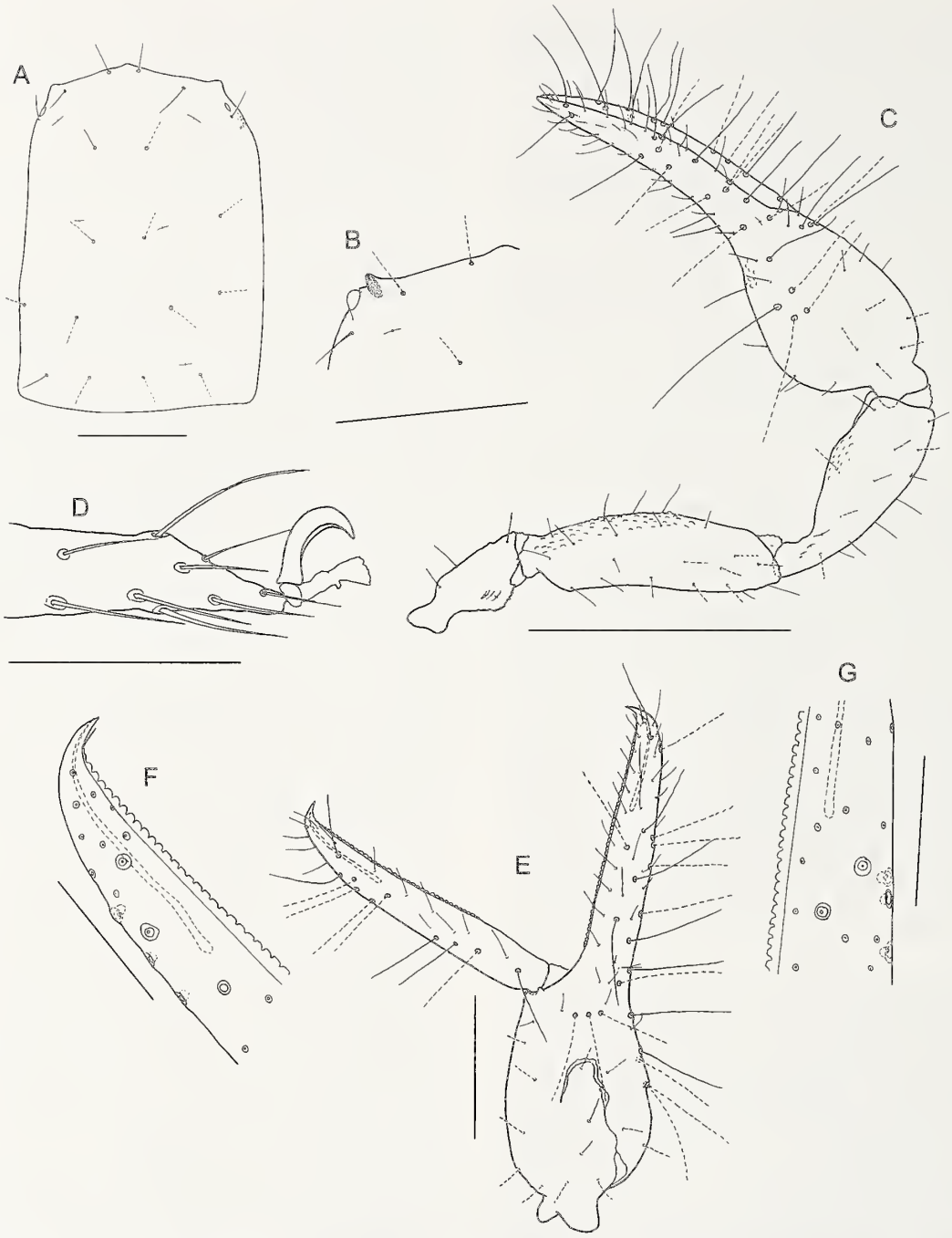

Figure 31.—*Typhloroncus planodentatus* Harvey & Muchmore sp. nov., male holotype, unless stated otherwise: A. Carapace, dorsal, male paratype (FSCA, WM3872.01001); B. Carapace, region of left eye, dorsal; C. Right pedipalp, dorsal; D. Tip of left tarsus IV, paratype female (FSCA, WM2103.01001); E. Left chela, lateral; F. Tip of movable chelal finger, lateral; G. fixed chelal finger, lateral. Scale lines = 0.5 mm (C); 0.2 mm (A, B); 0.1 mm (E–G).

(including 2 tactile setae): 2. Setae of tergites and sternites IX–XI acuminate. Anterior margin of anal operculum touching posterior margin of sternite XI (Fig. 30C).

Genitalia: male with median genital sac not visible in material examined. Female with large gonosac which is covered with scattered pores.

Dimensions (mm): Males: holotype followed by other males (where applicable): Body length ca. 1.65 (2.22). Pedipalp: trochanter 0.274/0.112 (0.335/0.127), femur 0.505/0.141 (0.672/0.147), patella 0.435/0.153 (0.573/0.165), chela (with pedicel) 0.918/0.265 (1.160/0.286), chela (without pedicel) 0.866 (1.090), hand (without pedicel) length 0.350 (0.435), movable finger length 0.538 (0.686). Chelicera 0.264, movable finger length 0.127. Carapace ?/? (damaged) (0.607/0.454); eye diameter 0.026 (0.016). Leg I: femur 0.243/0.076, patella 0.141/0.069, tibia 0.187/0.055, metatarsus 0.118/0.043, tarsus 0.202/0.038. Leg IV: femur + patella 0.444/0.201 (0.518/0.222), tibia 0.320/0.082, metatarsus 0.166/0.058, tarsus 0.266/0.042.

Female: Body length 2.13. Pedipalp: trochanter 0.298/0.128, femur 0.573/0.155, patella 0.461/0.166, chela (with pedicel) 1.003/0.320, chela (without pedicel) 0.942, hand (without pedicel) length 0.400, movable finger length 0.552. Chelicera 0.296/0.147, movable finger length 0.177. Carapace 0.551/? (distorted); eye diameter 0.026. Leg I: femur 0.273/0.084, patella 0.138/0.077, tibia 0.216/0.057, metatarsus 0.120/0.049, tarsus 0.203/0.030. Leg IV: femur + patella 0.201/0.193, tibia 0.347/0.087, metatarsus 0.170/0.062, tarsus 0.267/0.045.

Remarks.—*Typhloroncus planodentatus* is the first species of the genus to be found that possesses eyes, as all others, including the type species from the US Virgin Islands, completely lack eyes (Muchmore 1979, 1982b, 1986). The specimen from Mesa Llera differs from the other two specimens by having a substantially smaller eye diameter, 0.016 mm in the Mesa Llera specimen (Fig. 31B) and 0.026 mm in the others (Fig. 31A). However, we refrain from referring this specimen to a new species, as the differences are slight, and they have all been collected near each other.

Typhloroncus planodentatus has been found only on three occasions in the neighboring Mexican states of Tamaulipas and San Luis Potosí (Fig. 26E). Even though the hand-written slide label of the male holotype from San Luis Potosí clearly reads "20 MILES S. OF VALLEA", the locality is most likely south of Ciudad Valles. The collector of the specimen, L. Irby Davis, collected widely in the area during the late 1930s and to the mid–1940s (e.g., Archer 1953; Gertsch & Davis 1946; Lowery & Newman 1951), and the spelling on the slide label appears to be a minor transcription error.

Etymology.—The specific epithet refers to the flattened teeth of the fixed chelal finger, *planus*, Latin, even, flat, level, smooth, and *dentatus*, Latin, toothed, pointed (Brown 1956).

Typhloroncus troglobius Muchmore 1982
Fig. 26E

Typhloroncus troglobius Muchmore, 1982b:71–73, Figs. 24–26; Mahnert 1984a:677, Fig. 49; Muchmore 1986:28; Harvey 1991:322; Ceballos 2004:428; Harvey 2013:unpaginated.

Material examined.—*Holotype.* MEXICO: *Puebla*: female, Grutas de Atepolihuit, 5 km SW. of Cuetzalan (19°59′N, 97°33′W), 18 December 1976, J.R. Reddell, D. McKenzie, C. Solieau (FSCA, WM4676.01001).

Diagnosis.—*Typhloroncus troglobius* is a large, blind troglobite that differs from *T. attenuatus* by the lack of lanceolate setae on the leg tarsi, and from the other congeneric troglobites (*T. diabolus* and *T. xilitlensis*) in being slightly smaller, e.g., pedipalpal femur of female 2.03 mm long, and chela (without pedicel) of female 3.11 mm long, compared with femur 2.34–2.37 mm long and chela (with pedicel) 3.73–3.77 mm long in *T. diabolus* and *T. xilitlensis*.

Description.—*Adult:* See Muchmore (1982b) and Mahnert (1984a).

Remarks.—*Typhloroncus troglobius* was described by Muchmore (1982b) from a single female from Grutas de Atepolihuit, Mexico (Fig. 26E). Mahnert (1984a) provides an illustration of the chelal trichobothrial pattern.

Typhloroncus xilitlensis Muchmore 1986
Fig. 26E

Typhloroncus xilitlensis Muchmore 1986: 28–30, Figs. 20–21; Harvey 1991:322; Ceballos 2004:428; Harvey 2013:unpaginated.

Material examined.—*Holotype.* MEXICO: *San Luis Potosí*: female, Sótano de Huitzmolotitla, 2 km NNW. of Xilitla (21°25′N, 99°00′W), 4 January 1982, O. Kukal (FSCA, WM6104.01001).

Diagnosis.—*Typhloroncus xilitlensis* is a large, blind troglobite that differs from other congeneric troglobites as follows: from *T. attenuatus* by the lack of lanceolate setae on the leg tarsi, from *T. troglobius* by its larger size, e.g.,pedipalpal femur of female 2.37 mm long, and chela (without pedicel) of female 3.77 mm long, compared with 2.03 mm and 3.11 mm, respectively, and from *T. diabolus* is having more slender pedipalpal segments, e.g., pedipalpal femur of female 7.65 × longer than broad, and chela (without pedicel) of female 6.85 × longer than broad.

Description.—*Adult:* See Muchmore (1986).

Remarks.—*Typhloroncus xilitlensis* was described by Muchmore (1986) from a single female from Sótano de Huitzmolotitla, Mexico (Fig. 26E).

Genus *Xorilbia* Harvey & Mahnert 2006

Xorilbia Harvey & Mahnert 2006:228.

Type species.—*Ideoroncus arboricola* Mahnert 1979, by original designation.

Diagnosis.—*Xorilbia* resembles *Mahnertius*, *Typhloroncus* and *Dhanus siamensis* in having arolia that are shorter than the claws, and that also have a small hooked protuberance. Unlike these genera, *Xorilbia* has a divided arolium.

Description.—*Adult:* See Harvey & Mahnert (2006). In addition: base of fixed chelal finger without small denticles.

Nymphs: Pedipalps: *Tritonymph*: fixed finger with 15 trichobothria, movable finger with 8 trichobothria; *eb* region with 1 trichobothrium; *ib* region with 4 trichobothria; *ist* region with 3 trichobothria; *est* region with 4 trichobothria; *et* slightly distal to *it*; *b* region with 2 trichobothria; *t* region with 5 trichobothria. *Deutonymph*: not documented. *Protonymph: eb*, *et*, *ist* and *t* regions each with 1 trichobothrium; others absent.

Remarks.—*Xorilbia* occurs in the Amazonian region of northern Brazil and southern Venezuela (Figs. 2A, 26F).

KEY TO SPECIES OF *XORILBIA*

1. Fixed chelal finger with basal teeth forming broad lamella ..... *X. lamellifer*
   Fixed chelal finger with basal teeth not forming broad lamella 2
2. Teeth of movable chelal finger distinct ..... *X. arboricola*
   Teeth of movable chelal finger barely discernable ..... *X. gracilis*

Xorilbia arboricola (Mahnert 1979)
Fig. 26F

Ideoroncus arboricola Mahnert 1979:753–755, Figs. 70–74; Adis et al. 1987:488; Saturnino et al. 2009:35.
Albiorix arboricola (Mahnert): Mahnert 1984a:672–673; Mahnert 1985a:78; Mahnert & Adis 1986:213; Mahnert et al. 1986:Fig. 10; Harvey 1991:316; Adis & Mahnert 1993:Fig. 5; Mahnert & Adis 2002:379, Fig. 10; Adis et al. 2002:5; Aguiar et al. 2006:796, etc.
Xorilbia arboricola (Mahnert): Harvey & Mahnert 2006:229; Harvey 2013 unpaginated.
Albiorix aff. *arboricola* (Mahnert): Mahnert 1984a:673 (see *Albiorix gracilis* Mahnert).

Material examined.—None.

Diagnosis.—*Xorilbia arboricola* lacks the broad dental lamella of the fixed chelal finger found in *X. lamellifer* and has distinct teeth on the movable chelal finger (Mahnert 1979, 1984a).

Description.—*Adult:* See Mahnert (1979, 1984a).

Remarks.—This species was originally described as a species of *Ideoroncus*, but transferred to *Albiorix* when it was found to have divided arolia (Mahnert 1984a). It was transferred to the new genus *Xorilbia* by Harvey & Mahnert (2006) and is known from the Brazilian states of Amazonas and Pará (Fig. 26F).

Xorilbia gracilis (Mahnert 1985)
Fig. 26F

Albiorix aff. *arboricola* (Mahnert): Mahnert 1984a:673.
Albiorix gracilis Mahnert 1985b:223–224, Figs. 27–28; Mahnert & Adis 1986:213; Adis and Mahnert 1990:13, Figs. 2–3; Harvey 1991:317; Adis & Mahnert 1993:435, Figs. 2–3, 5; Mahnert & Adis 2002:379; Adis et al. 2002:5; Aguiar et al. 2006:795, 796, etc.; Saturnino et al. 2009:35.
Xorilbia gracilis (Mahnert): Harvey & Mahnert 2006:229–230.
Xorilbia cf. *gracilis* (Mahnert): Turienzo et al. 2010:561, 584–585.

Material examined.—See Harvey & Mahnert (2006).

Diagnosis.—*Xorilbia gracilis* lacks the broad dental lamella of the fixed chelal finger found in *X. lamellifer* and has barely discernible teeth on the movable chelal finger (Mahnert 1985b).

Description.—*Adult:* See Mahnert (1985b).

Nymphs: See Mahnert (1985b).

Remarks.—This species was originally described in the genus *Albiorix* (Mahnert 1985b), but was transferred to the new genus *Xorilbia* by Harvey & Mahnert (2006). It is only known from the Brazilian state of Amazonas, and the Venezuelan state of the same name (Harvey & Mahnert 2006) (Fig. 26F).

Xorilbia lamellifer (Mahnert 1985)
(Fig. 26F)

Albiorix lamellifer Mahnert 1985:224–225, Figs. 29–31; Mahnert & Adis 1986:213; Harvey 1991:317; Mahnert & Adis 2002:379; Saturnino et al. 2009:36.
Xorilbia lamellifer (Mahnert): Harvey & Mahnert 2006:230, Fig. 1; Harvey 2013:unpaginated.

Material examined.—See Harvey & Mahnert (2006).

Diagnosis.—*Xorilbia lamellifer* differs from the other two species of the genus by the fusion of the basal teeth of the fixed chelal finger into a broad lamella (Mahnert 1985b, Fig. 31).

Description.—*Adult:* See Mahnert (1985b).

Remarks.—This species was originally described in *Albiorix* (Mahnert 1985b), but was transferred to the new genus *Xorilbia* by Harvey & Mahnert (2006). It is only known from the Brazilian state of Amazonas (Fig. 26F).

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LITERATURE CITED

Adis, J., A.B. Bonaldo, A.D. Brescovit, R. Bertani, J.C. Cokendolpher, B. Condé, A.B. Kury, W.R. Lourenço, V. Mahnert, R. Pinto-da-Rocha, N.I. Platnick, J.R. Reddell, C.A. Rheims, L.S. Rocha, J.M. Rowland, P. Weygoldt & S. Woas. 2002. Arachnida at 'Reserva Ducke', central Amazonia/Brazil. Amazoniana 17:1–14.

Adis, J., W.J. Junk & N.D. Penny. 1987. Material zoológico depositado nas coleçoes sistemáticas de entomologia do INPA, resultante do "Projeto INPA/Max-Planck". Acta Amazonica 15:481–504.

Adis, J. & V. Mahnert. 1990. Vertical distribution and abundance of pseudoscorpion species (Arachnida) in the soil of a neotropical secondary forest during the dry and the rainy season. Acta Zoologica Fennica 190:11–16.

Adis, J. & V. Mahnert. 1993. Vertical distribution and abundance of pseudoscorpions (Arachnida) in the soil of two different neotropical primary forests during the dry and rainy seasons. Memoirs of the Queensland Museum 33:431–440.

Aguiar, N.O., T.L. Gualberto & E. Franklin. 2006. A medium-spatial scale distribution pattern of Pseudoscorpionida (Arachnida) in a gradient of topography (altitude and inclination), soil factors, and litter in a central Amazonia forest reserve, Brazil. Brazilian Journal of Biology 66:791–802.

Archer, A.F. 1953. Studies in the orbweaving spiders (Argiopidae). 3. American Museum Novitates 1622:1–27.

Balzan, L. 1887. Chernetidae nonnullae Sud-Americanae, II. Privately published, Asuncion.

Balzan, L. 1890. Revisione dei Pseudoscorpioni del Bacino dei Fiumi Paranà e Paraguay nell'America meridionale. Annali del Museo Civico di Storia Naturale di Genova (2a) 9:401–454.

Balzan, L. 1892. Voyage de M. E. Simon au Venezuela (Décembre 1887–Avril 1888). Arachnides. Chernetes (Pseudoscorpiones). Annales de la Société Entomologique de France 60:513–552.

Banks, N. 1898. Arachnida from Baja California and other parts of Mexico. Proceedings of the California Academy of Sciences (3) 1:205–308.

Beier, M. 1931. Neue Pseudoscorpione der U. O. Neobisiinea. Mitteilung aus dem Zoologischen Museum in Berlin 17:299–318.

Beier, M. 1932a. Pseudoscorpionidea - Afterskorpione. Pp. 117–192. *In* Handbuch der Zoologie. (W. Kükenthal & T. Krumbach, eds.). Vol. 3 (2) (5). Walter de Gruyter & Co., Berlin und Leipzig.

Beier, M. 1932b. Pseudoscorpionidea I. Subord. Chthoniinea et Neobisiinea. Tierreich 57:i–xx, 1–258.

Beier, M. 1955. Pseudoscorpionidea, gesammelt während der schwedischen Expeditionen nach Ostafrika 1937–38 und 1948. Arkiv för Zoologi (2) 7:527–558.

Beier, M. 1963. Eine neue Art der Pseudoscorpioniden-Gattung *Albiorix* aus Höhle Acuitlapan, Gro., Mexico. Ciencia, México 22:133–134.

Beier, M. 1964. Die Pseudoscorpionidcn-Fauna Chiles. Annalen des Naturhistorischen Museums in Wien 67:307–375.

Beier, M. 1970. Myrmecophile Pseudoskorpione aus Brasilien. Annalen des Naturhistorischen Museums in Wien 74:51–56.

Beier, M. 1974. Brasilianische Pseudoscorpione aus dem Museum in Genf. Revue Suisse de Zoologie 81:899–909.

Brown, R.W. 1956. Composition of scientific words. Revised edition. Smithsonian Institution Press, Washington, D.C.

Ceballos, A. 2004. Pseudoscorpionida. Pp. 417–429. *In* Biodiversidad, taxonomía y biogeografía de Artrópodos de México: hacia una síntesis de su conocimiento. (J.L. Bousquets, J.J. Morrone, O.Y. Ordóñez & I.V. Fernández, eds.). Vol. 4. Facultad de Ciencias, UNAM, México, D.F.

Ceballos, A., B. Ferradas & Rosso de. 2008. Pseudoscorpiones. Pp. 105–116. *In* Biodiversidad de Artrópodos Argentinos. (L.E. Claps, G. Debandi & S. Roig-Juñent, eds.). Vol. 2. Sociedad Entomológica Argentina, Mendoza.

Cekalovic, K.T. 1984. Catalogo de los Pseudoscorpiones y Palpigradi de Chile (Chelicerata). Boletín de la Sociedad de Biología de Concepción 55:7–35.

Chamberlin, J.C. 1923. New and little known pseudoscorpions, principally from the islands and adjacent shores of the Gulf of California. Proceedings of the California Academy of Sciences (4) 12:353–387.

Chamberlin, J.C. 1930. A synoptic classification of the false scorpions or chela-spinners, with a report on a cosmopolitan collection of the same. Part II. The Diplosphyronida (Arachnida-Chelonethida). Annals and Magazine of Natural History (10) 5:1–48, 585–620.

Chamberlin, J.C. 1931. The arachnid order Chelonethida. Stanford University Publications, Biological Sciences 7:1–284.

Chamberlin, J.C. 1946. The genera and species of the Hyidae, a family of the arachnid order Chelonethida. Bulletin of the University of Utah, Biological Series 96:1–16.

Eisen, G. 1895. Explorations in the Cape Region of Baja California in 1894, with references to former expeditions of the California Academy of Sciences. Proceedings of the California Academy of Sciences (2) 5:733–775.

Ellingsen, E. 1905. On some pseudoscorpions from South America in the collection of Prof. F. Silvestri. Zoologischer Anzeiger 29:323–328.

Ellingsen, E. 1910. Die Pseudoskorpione des Berliner Museums. Mitteilung aus dem Zoologischen Museum in Berlin 4:357–423.

Feio, J.L. & de Araújo. 1945. Novos pseudoscorpiões de região neotropical (com a descriçao de uma subfamilia, dois géneros e sete espécies). Boletim do Museu Nacional Rio de Janeiro, n.s. Zoologia 44:1–47.

Gertsch, W.J. & L.I. Davis. 1937. Report on a collection of spiders from Mexico. I. American Museum Novitates 961:1–29.

Gertsch, W.J. & L.I. Davis. 1946. Report on a collection of spiders from Mexico. V. American Museum Novitates 1313:1–12.

Harvey, M.S. 1987. A revision of the genus *Synsphyronus* Chamberlin (Garypidae: Pseudoscorpionida: Arachnida). Australian Journal of Zoology, Supplementary Series 126:1–99.

Harvey, M.S. 1991. Catalogue of the Pseudoscorpionida. Manchester University Press, Manchester.

Harvey, M.S. 1992. The phylogeny and classification of the Pseudoscorpionida (Chelicerata: Arachnida). Invertebrate Taxonomy 6:1373–1435.

Harvey, M.S. 2011. Two new species of *Synsphyronus* (Pseudoscorpiones: Garypidae) from southern Western Australian granite landforms. Records of the Western Australian Museum 26:11–22.

Harvey, M.S. 2013. Pseudoscorpions of the World, version 3.0. Western Australian Museum, Perth. Online at http://www.museum.wa.gov.au/catalogues/pseudoscorpions/ (accessed 24 August 2013.

Harvey, M.S., R. Barba, D., W.B. Muchmore & A. Peréz, G. 2007. *Pseudalbiorix*, a new genus of Ideoroncidae (Pseudoscorpiones, Neobisioidea) from central America. Journal of Arachnology 34:610–626.

Harvey, M.S. & K.L. Edward. 2007. A review of the pseudoscorpion genus *Ideoblothrus* (Pseudoscorpiones, Syarinidae) from western and northern Australia. Journal of Natural History 41:445–472.

Harvey, M.S. & V. Mahnert. 2006. The systematic position of the Amazonian species of *Albiorix* (Pseudoscorpiones, Ideoroncidae). Journal of Arachnology 34:227–230.

Harvey, M.S., P.B. Ratnaweera, P.V. Randeniya & M.R. Wijesinghe. 2012. A new species of the pseudoscorpion genus *Megachernes* (Pseudoscorpiones: Chernetidae) associated with a threatened Sri Lankan rainforest rodent, with a review of host associations of *Megachernes*. Journal of Natural History 46:2519–2535.

Harvey, M.S. & E.S. Volschenk. 2007. The systematics of the Gondwanan pseudoscorpion family Hyidae (Pseudoscorpiones: Neobisioidea): new data and a revised phylogenetic hypothesis. Invertebrate Systematics 21:365–406.

Hoff, C.C. 1945. The pseudoscorpion genus *Albiorix* Chamberlin. American Muscum Novitates 1277:1–12.

Hoff, C.C. 1949. The pseudoscorpions of Illinois. Bulletin of the Illinois Natural History Survey 24:407–498.

Hoff, C.C. 1950. Pseudoescorpionidos nuevos o poco conocidos de la Argentina (Arachnida, Pseudoscorpionida). Arthropoda, Buenos Aires 1:225–237.

Hoff, C.C. 1956. Diplosphyronid pseudoscorpions from New Mexico. American Museum Novitates 1780:1–49.

Hoff, C.C. 1958. List of the pseudoscorpions of North America north of Mexico. American Museum Novitates 1875:1–50.

Hoff, C.C. 1959. The ecology and distribution of the pseudoscorpions of north-central New Mexico. University of New Mexieo Publications in Biology 8:1–68.

International Commission on Zoological Nomenclature. 1999. International code of zoological nomenclature, fourth edition. International Trust for Zoological Nomenclature, London.

Judson, M.L.I. 2007. A new and endangered species of the pseudoseorpion genus *Lagynochthonius* from a cave in Vietnam, with notes on chelal morphology and the composition of the Tyrannochthoniini (Arachnida, Chelonethi, Chthoniidae). Zootaxa 1627:53–68.

Lowery, G.H., Jr. & R.J. Newman. 1951. Notes on the ornithology of southeastern San Luis Potosí. Wilson Bulletin 63:315–322.

Mahnert, V. 1979. Pseudoskorpione (Arachnida) aus dem Amazonas-Gebiet (Brasilien). Revue suisse de Zoologie 86:719–810.

Mahnert, V. 1981a. Die Pseudoskorpione (Arachnida) Kenyas. I. Neobisiidae und Ideoroncidae. Revue Suisse de Zoologie 88:535–559.

Mahnert, V. 1981b. Sigles trichobothriaux chez les pseudoscorpions (Arachnida). Memorie, Atti della Società Toscana di Scienze Naturali residente in Pisa B 88 supplemento:185–192.

Mahnert, V. 1984a. Beitrag zu einer besseren Kenntnis der Ideoroneidae (Arachnida: Pseudoscorpiones), mit Beschreibung von sechs neuen Arten. Revue Suisse de Zoologie 91:651–686.

Mahnert, V. 1984b. Forschungen an der Somalilandküste. Am Strand und auf den Dünen bei Sar Uanle. 36. Pseudoscorpiones (Arachnida). Monitore Zoologico Italiano, n.s., Supplemento 19:43–66.

Mahnert, V. 1985a. Pseudoscorpions (Arachnida) from the lower Amazon region. Revista Brasileira de Entomologia 29:75–80.

Mahnert, V. 1985b. Weitere Pseudoskorpione (Arachnida) aus dem zentralen Amazonasgebiet (Brasilien). Amazoniana 9:215–241.

Mahnert, V. 2001. Cave-dwelling pseudoscorpions (Arachnida, Pseudoscorpiones) from Brazil. Revue Suisse de Zoologie 108:95–148.

Mahnert, V. & J. Adis. 1986. On the occurrence and habitat of Pseudoscorpiones (Arachnida) from Amazonian forest of Brazil. Studies on Neotropical Fauna and Environment 20:211–215.

Mahnert, V. & J. Adis. 2002. Pseudoscorpiones. Pp. 367–380. *In* Amazonian Arachnida and Myriapoda. (J. Adis, ed.). Pensoft Publishers, Sofia.

Mahnert, V., J. Adis & P.F. Bührnheim. 1986. Key to the families of Amazonian Pseudoscorpiones (Arachnida). Amazoniana 10:21–40.

Mahnert, V., O. Di Iorio, P. Turienzo & A. Porta. 2011. Pseudoscorpions (Arachnida) from Argentina. New records of distributions and habitats, corrections and an identification key. Zootaxa 2881:1–30.

Muchmore, W.B. 1972. New diplosphyronid pseudoscorpions, mainly cavernicolous, from Mexico (Arachnida, Pseudoscorpionida). Transactions of the American Microscopical Society 91:261–276.

Muchmore, W.B. 1979. Pseudoscorpions from Florida and the Caribbean area. 9. *Typhloroncus*, a new genus from the Virgin Islands (Ideoroncidae). Florida Entomologist 62:317–320.

Muchmore, W.B. 1982a. Pseudoscorpionida. Pp. 96–102. *In* Synopsis and classification of living organisms. (S.P. Parker, ed.). Vol. 2. McGraw-Hill, New York.

Muchmore, W.B. 1982b. Some new species of pseudoscorpions from caves in Mexico (Arachnida, Pseudoscorpionida). Bulletin for the Association of Mexican Cave Studies 8:63–78.

Muchmore, W.B. 1986. Additional pseudoscorpions, mostly from caves, in Mexico and Texas (Arachnida: Pseudoscorpionida). Texas Memorial Museum, Speleological Monographs 1:17–30.

Muchmore, W.B. 1993. List of terrestrial invertebrates of St. John, U.S. Virgin Islands (exclusive of Acarina and Insecta), with some records of freshwater species. Caribbean Journal of Science 29:30–38.

Muchmore, W.B. 1998. Review of the family Bochicidae, with new species and records (Arachnida: Pseudoscorpionida). Insecta Mundi 12:117–132.

Muchmore, W.B. & R.B. Pape. 1999. Description of an eyeless, cavernicolous *Albiorix* (Pseudoscorpionida: Ideoroncidae) in Arizona, with observations on its biology and ecology. Southwestern Naturalist 44:138–147.

Murienne, J., M.S. Harvey & G. Giribet. 2008. First molecular phylogeny of the major clades of Pseudoscorpiones (Arthropoda: Chelicerata). Molecular Phylogenetics and Evolution 49:170–184.

Murthy, V.A. & T.N. Ananthakrishnan. 1977. Indian Chelonethi. Oriental Insects Monograph 4:1–210.

Reddell, J.R. 1981. A review of the cavernicole fauna of Mexico, Guatemala and Belize. Bulletin of the Texas Memorial Museum 27:1–327.

Redikorzev, V. 1938. Les pseudoscorpions de l'Indochine française recueillis par M.C. Dawydoff. Mémoires du Muséum National d'Histoire Naturelle, Paris 10:69–116.

Roewer, C.F. 1936. Chelonethi oder Pseudoskorpione. Pp. 1–160. *In* Bronn's Klassen und Ordnungen des Tierreichs. (H.G. Bronns, ed.). Vol. 5(IV)(6)(1). Akademische Verlagsgesellschaft M.B.H, Leipzig.

Roewer, C.F. 1937. Chelonethi oder Pseudoskorpione. Pp. 161–320. *In* Bronn's Klassen und Ordnungen des Tierreichs. (H.G. Bronns, ed.). Vol. 5(IV)(6)(1). Akademische Verlagsgesellschaft M.B.H, Leipzig.

Rowland, J.M. & J.R. Reddell. 1976. Annotated checklist of the arachnid fauna of Texas (excluding Acarida and Araneida). Occasional Papers of the Museum, Texas Technical University 38:1–25.

Saturnino, R., A.L. Tourinho, C.S. de Azevedo & C. Magalhães. 2009. Catalogue of type specimens of invertebrates in the collection of the Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil. IV. Arachnida: Acari, Palpigradi, Pseudoscorpiones, Ricinulei and Schizomida. Zootaxa 1973:28–40.

Turienzo, P., O. di Iorio & V. Mahnert. 2010. Global checklist of pseudoscorpions (Arachnida) found in birds' nests. Revue Suisse de Zoologie 117:557–598.

Vachon, M. 1949. Ordre des Pseudoscorpions. Pp. 437–481, *In* Traité de zoologie. (P.-P. Grassé, ed.). Vol. 6. Masson, Paris.

Vachon, M. 1958. Sur deux Pseudoscorpions nouveaux des cavernes de l'Afrique équatoriale [Ideoroncidae]. Notes Biospéologiques 13:57–66.

Vachon, M. 1964. Sur l'établissement de formules précisant l'ordre d'apparition des trichobothries au cours du développement post-embryonnaire chez les Pseudoscorpions (Arachnides). Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris 258:4839–4842.

Villegas-Guzmán, G.A. 2006. Pseudoescorpiones (Arachnida: Pseudoscorpiones) de la zona de restauración ecológia "El Cartón", Frontera Corozal, Chiapas. Pp. 133–135. *In* Entomología Mexicana. (V.E.G. Estrada, J. Romero, N., A. Equihua, M., C. Luna, L. & J. Rosas, A., eds.). Vol. 5 (1). Manzanillo, Colima.

Villegas-Guzmán, G.A. & O.F. Francke. 2009. Description of the male of the genus *Typhloroncus* Muchmore, 1979 (Pseudoscorpiones: Ideoroncidae). Texas Memorial Museum Speleological Monographs 7:63–66.

Vitali-di Castri, V. 1963. La familia Vachoniidae (= Gymnobisiidae) en Chile (Arachnidea, Pseudoscorpionida). Investigaciones Zoológicas Chilenas 10:27–82.

Vitali-di Castri, V. 1965. *Cheiridium danconai* n. sp. (Pseudoscorpionida) con consideraciones sobre su desarrollo postembrionario. Investigaciones Zoológicas Chilenas 12:67–92.

With, C.J. 1905. On Chelonethi, chiefly from the Australian region, in the collection of the British Museum, with observations on the "coxal sac" and on some cases of abnormal segmentation. Annals and Magazine of Natural History (7) 15:94–143, 328.

With, C.J. 1906. The Danish expedition to Siam 1899–1900. III. Chelonethi. An account of the Indian false-scorpions together with studies on the anatomy and classification of the order. Oversigt over det Konigelige Danske Videnskabernes Selskabs Forhandlinger (7) 3:1–214.

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On the enigmatic genus *Philora*: familial assignment and taxonomic revision (Opiliones: Laniatores: Stygnopsidae)

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Abstract. The harvestman genus *Philora* Goodnight & Goodnight 1954 and the type species *P. tuxtlae* are redescribed, and *Philora quetzalzin* new species is described. The genus is newly assigned to the family Stygnopsidae Sørensen 1932 based on external morphology and male genitalia, which are described herein for the first time. The genus is compared with the morphologically similar genera *Paramitraceras* Pickard-Cambridge 1905, *Sbordonia* Šilhavý 1977, and *Troglostygnopsis* Šilhavý 1974 sensu stricto. *Philora* is unique within the family in having a scutum completum. The presence of a scutum completum in *Philora* and others laniatoreans is discussed. The male genitalia of the genera *Paramitraceras*, *Philora*, *Troglostygnopsis* and presumably the genus *Sbordonia*, are very similar and share a morphological pattern described here as the Paramitraceras-pattern.

Keywords: Mexico, Stygnopsidae, new species, scutum completum, male genitalia

There are 66 genera and 92 species without familial assignment (incertae sedis) within the harvestman suborder Laniatores Thorell 1876, representing 4.8% and 2.2% of the total diversity of the suborder (Kury 2011). Recently, some genera listed as incertae sedis or with predetermined familial assignment have been transferred to different families, based on morphological characters (particularly male genitalia) or based on eladistic analyses (Pinto-da-Rocha & Hara 2009; Pérez-González 2011; Kury 2012; Villareal & Kury 2012). The monotypic genus *Philora* Goodnight & Goodnight 1954 and its type species *P. tuxtlae* was described from material collected near the San Martin Volcano, Los Tuxtlas, Veracruz in Mexico. The authors indicated that this genus is related to *Paramitraceras* Pickard-Cambridge 1905, differing only by a lower tarsal count of 2(1):2(1):4:4 in *Philora* versus 3(2):4(2):5:5 in *Paramitraceras*. Initially, this genus was assigned to the subfamily Phalangodinae Simon 1879 of the family Phalangodidae Simon 1879, a familial assignment based on few, poorly understood external morphological characters, and the genus was later regarded as incertae sedis until adequately reviewed in a modern context (Kury & Cokendolpher 2000; Kury 2003).

Recently we made several collecting trips to the rainforests of the Los Tuxtlas region, and have collected adult specimens of *P. tuxtlae* from the type locality. In addition, specimens of a second species of the genus, described herein, were collected in the western region of the state of Veracruz. The male genitalia of the two species assigned to *Philora* have an internal capsule forming a follis on the ventral side in dorsal view of the pars distalis, with a few distal espiniform projections and with several setae on the pars distalis; this morphology corresponds to the general pattern of the family Stygnopsidae Sørensen 1932, and also shows great similarity to the male genitalia of the genus *Paramitraceras* (Pérez-González 2006; Cruz-López & Francke 2012, 2013).

Using the external morphology and male genitalia of the two species, we revise the diagnosis of the genus, newly transfer the genus to the family Stygnopsidae, and discuss and describe the Paramitraceras-pattern of the male genitalia, present in the genera *Paramitraceras*, *Philora*, the type species of the genus *Troglostygnopsis* Šilhavý 1974, and probably in the genus *Sbordonia* Šilhavý 1977.

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METHODS

The material examined is deposited in the Colección Nacional de Arácnidos (CNAN), Instituto de Biología, Universidad Nacional de México (UNAM), Mexico. We made photos using a Hitachi SU1510 Scanning Electronic Microscope (SEM) and a Nikon Coolpix S10 VR camera. Photographs were edited using PhotoShop CS5 software. Male genitalia nomenclature follows Cruz-López & Francke (2013).

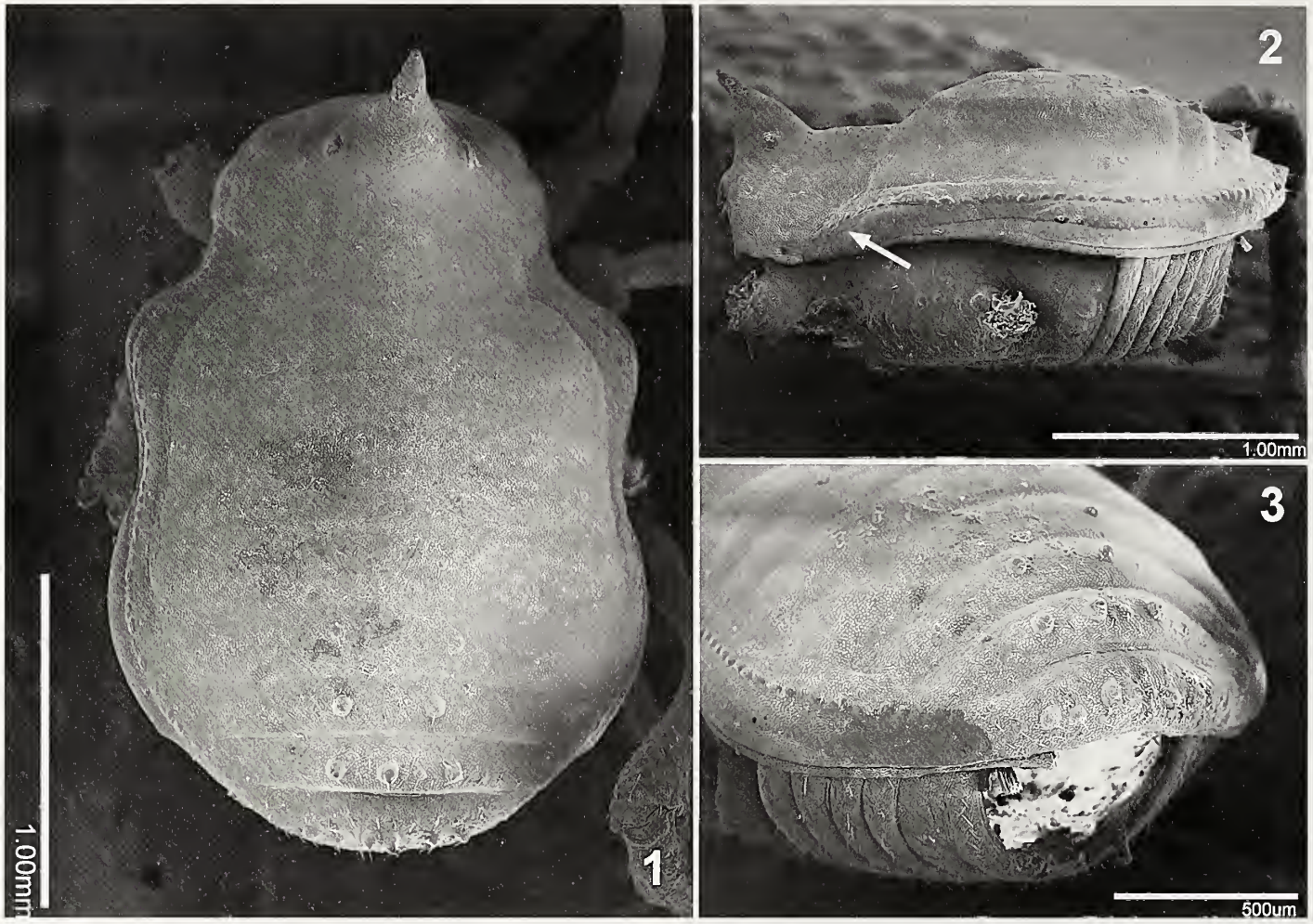
TAXONOMY

Family Stygnopsidae Sørensen 1932
Genus *Philora* Goodnight & Goodnight 1954

Philora Goodnight & Goodnight 1954:345; Kury & Cokendolpher 2000:154; Kury 2003:27.

Type species.—*Philora tuxtlae* Goodnight & Goodnight 1954, by original designation

Emended diagnosis.—Small stygnopsids, 3 mm maximum length. Scutum completum with numerous light-colored areas on sides (Figs. 1, 17, 33–36). Setiferous tubercles on pedipalps with bases conical, setae inserted basally (Figs. 8, 9, 43). Metatarsus IV dorsally with one prominent setiferous tubercle distally, with one or two apical setae (Figs. 44, 46). Pars distalis with Paramitraceras-pattern (as defined herein), with 6 to 10 pairs of lateral setae, arranged in two groups; these setae originating basally or laterally to follis. Pars distalis ventroapically with two pairs of setae, paramedian pair are represented by two microsetae close to each other; lateral pair large, pointing basally. Lobes of the dorsal bilobular projection wing-shaped, apex points basally; ventroapical margin of pars distalis with two lateral spiniform projections (Figs. 12–14, 28–32). Tarsal count low, 2:2:4:4, distitarsi I and II with one subarticle only. Males with four light-colored, pointed areas in the stigmatic region (Figs. 37–40).



Figures 1–3.—*Philora tuxtlae* Goodnight & Goodnight 1954, male. 1. Habitus dorsal view; 2. Habitus lateral view (arrow points to anterior lateral light-colored areas); 3. Habitus dorso-posterior view.

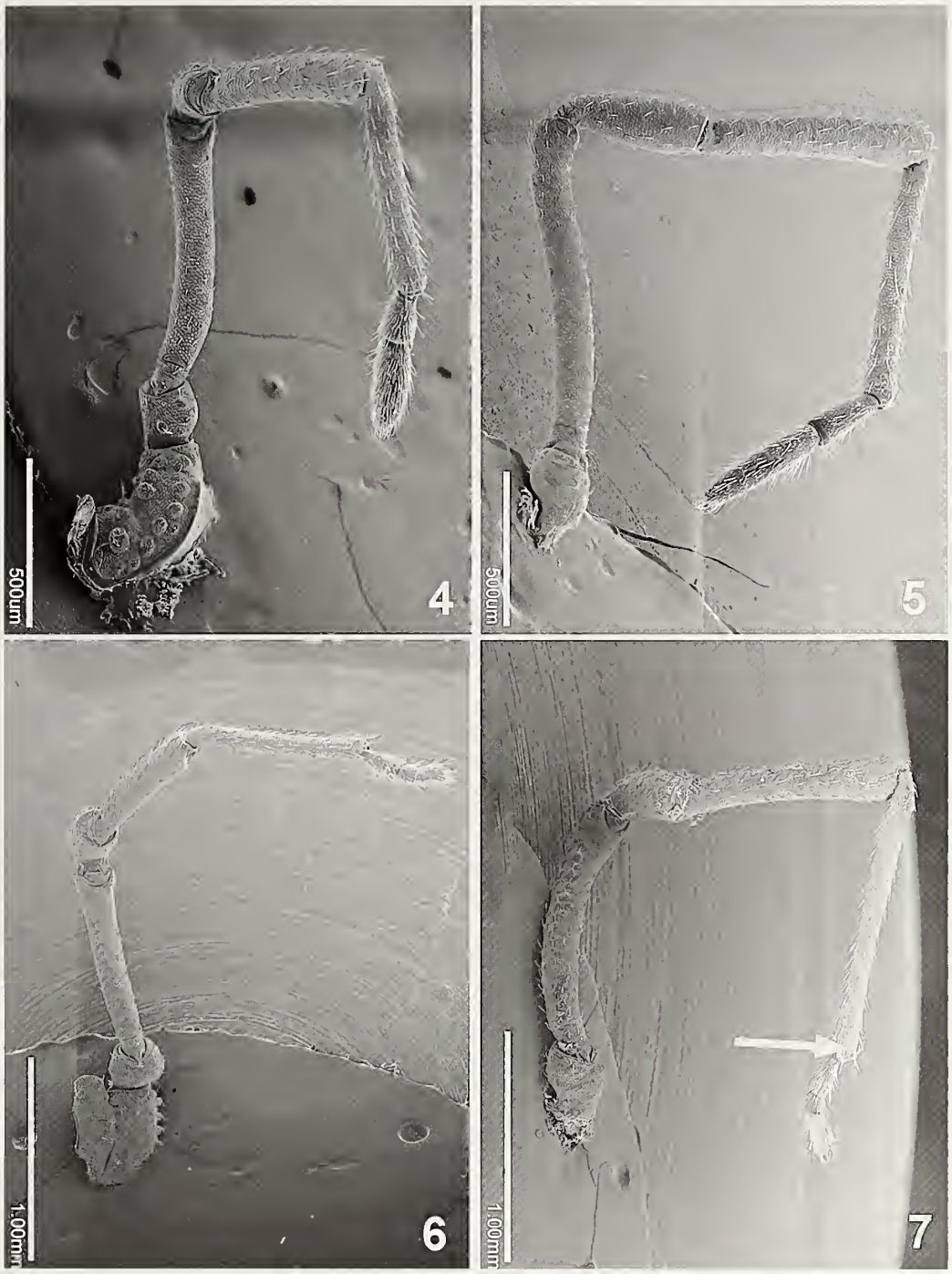
Philora tuxtlae Goodnight & Goodnight 1954
(Figs. 1–16, 33, 36–38, 41–44)

Philora tuxtlae Goodnight & Goodnight 1954:346, Figs. 1, 2; Kury & Cokendolpher 2000:154; Kury 2003:27.

Type data.—MEXICO: *Veracruz*, Holotype male?, and paratypes males or females? (see Remarks), San Martín volcano, 1050 m, 12 km N of San Andrés Tuxtla, Municipio San Andrés Tuxtla (deposited in American Museum of Natural History, New York; not examined).

Material examined.—MEXICO: *Veracruz*, 1 ♀, Estación Biológica Tropical de "Los Tuxtlas", UNAM, Municipio San Andrés Tuxtla (18°34′47.399″N, 95°04′53.399″W, 429 m.), 27 August 2005, O. Francke, A. Valdez, H. Montaño, M. Córdoba, A. Jaimes (CNAN); 1 ♂, same data, 11 January 2012, O. Francke, G. Montiel, J. Cruz, R. Monjaraz (CNAN); 8 ♂, 9 ♀, 6 juveniles, same data, 10 November 2012, O. Francke, G. Montiel, A. Valdez, J. Cruz, R. Monjaraz (CNAN); 5 ♂, 10 ♀, 5 juveniles, 1 km SE. of Díaz Ordaz, Municipio San Andrés Tuxtla (18°31′39.899″N, 95°05′12.875″W, 480 m), 10 November 2012, O. Francke, G. Montiel, A. Valdez, J. Cruz, R. Monjaraz (CNAN); 3 ♀, 2 juveniles, 1.5 km E of Ejido "La Perla de San Martín", Municipio Catemaco (18°33′19.800″N, 95°07′16.103″W, 749m), 11 November 2012, O. Francke, G. Montiel, A. Valdez, J. Cruz, R. Monjaraz (CNAN); 2 ♀, 1 juvenile, 3 km W of Ejido Ruíz Cortines, Municipio Catemaco (18°31′24.852″N, 95°08′27.780″W, 1,152 m), 11 November 2012, O. Francke, G. Montiel, A. Valdez, J. Cruz, R. Monjaraz (CNAN).

Diagnosis.—*Philora tuxtlae* differs from *P. quetzalzin* in having a narrow ocularium, with a noticeably pointed apex. The dorsal ornamentation is composed of minute tubercles in *P. tuxtlae* (Fig. 1), but has larger tubercles in *P. quetzalzin* (Fig. 17); the posterior tergites with the medial spiniform tubercles markedly larger than the rest of the dorsum in *P. tuxtlae* (Figs. 1–3), whereas they are uniform in size in *P. quetzalzin* (Fig. 17–19). The sexual dimorphism in *P. tuxtlae* is only in the coloration and shape of the stigmatic region (Figs. 37, 38); whereas in *P. quetzalzin*, the sexual dimorphism is in the coloration and the shape of stigmatic region and the chelieeral size (seutum/cheliceral hand ratio: 2.8 in males, vs. scutum/cheliceral hand ratio: 3.1 in females), and the shape of ocularium (Figs. 33, 34, 39, 40). Males of *P. tuxtlae* have a small dorsodistal tubercle on metatarsus IV (Figs. 7, 44), which is larger and mesally in *P. quetzalzin* (Figs. 23, 46). The 12 setae of the pars distalis originate lateral to the follis, and are in two distinctive groups of three setae (basal and lateral) on each side in *P. tuxtlae* (Figs. 12–14); whereas they number 20, with 10



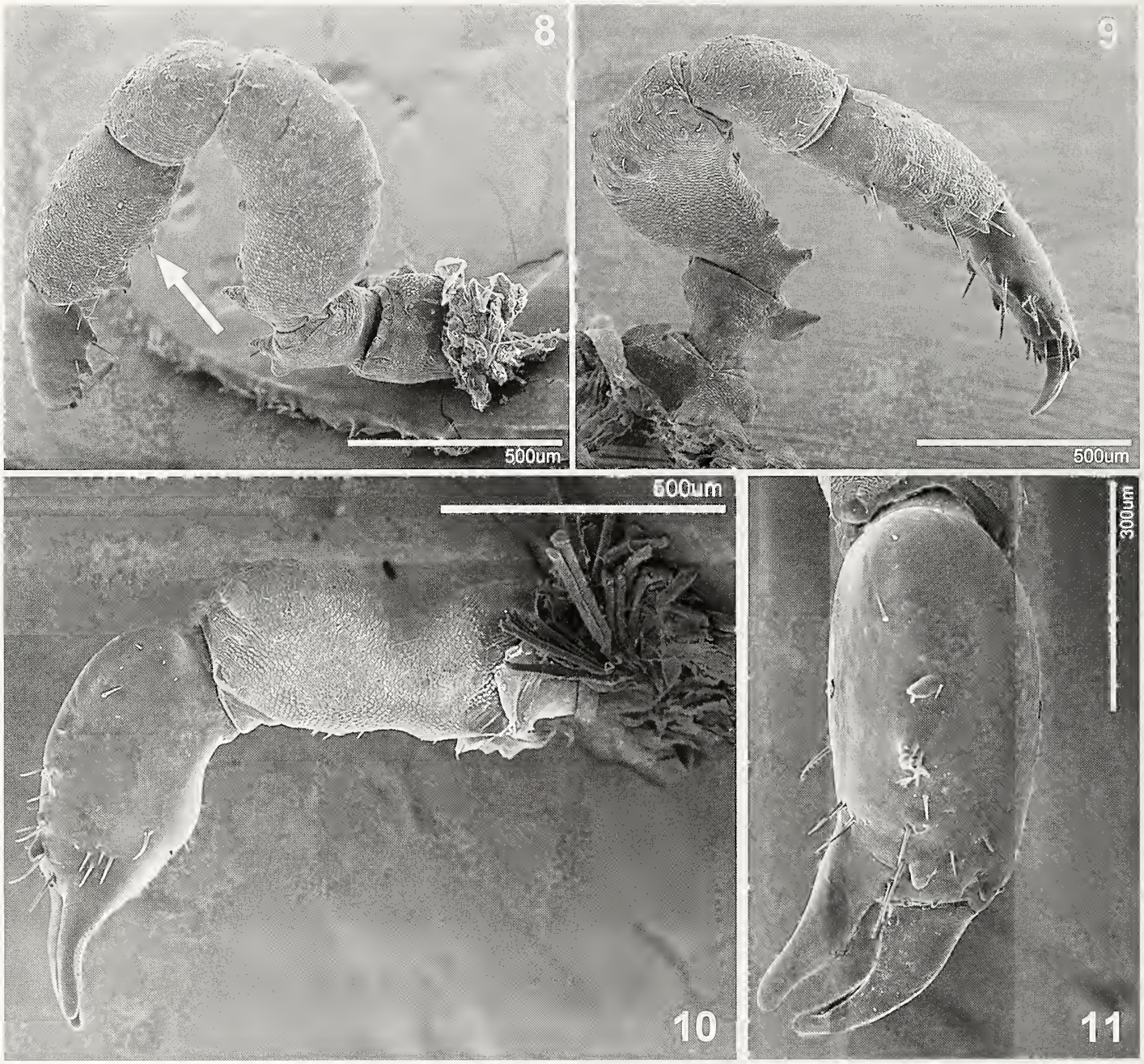
Figures 4–7.—*Philora tuxtlae* Goodnight & Goodnight 1954, male. 4. Leg I mesal view; 5. Leg II mesal view; 6. Leg III mesal view; 7. Leg IV mesal view (arrow points to dorsodistal setiferous tubercle).

seattered setae on each side in *P. quetzalzin* (Figs. 28–32). The ventroapical macrosetae of the pars distalis is stouter in *P. quetzalzin* (Figs. 31, 32), than in *P. tuxtlae* (Figs. 14, 15).

Redescription.—*Male:* Measurements (based on a male from Estación Biológica Tropical "Los Tuxtlas"): Scutum length: 2.3, scutum width: 1.3. Dorsum: Scutum covered by very small tubercles, equally sized on all dorsum, with few setae. Posterior tergites with medial tubercles noticeably developed, rounded. Ocularium conical, basal area small, pointed distally, without posterior bulge (Figs. 1–3).

Venter: Densely covered by spiniform setae. Coxa I with 1 median, irregular row of small, setiferous tubercles. Free sternites with setae similar to the rest of ventral region, but more densely covered. Stigmatic area with 4 differentiated light-colored areas, 2 posterior areas slightly closer to each other than anterior pair (Fig. 37). Anal plate with some rounded tubercles.

Chelicera: Scutum/cheliceral hand ratio: 4, with 3 to 4 setiferous spiniform tubercles on the frontal side, slightly developed. Cheliceral teeth present only on fixed finger,



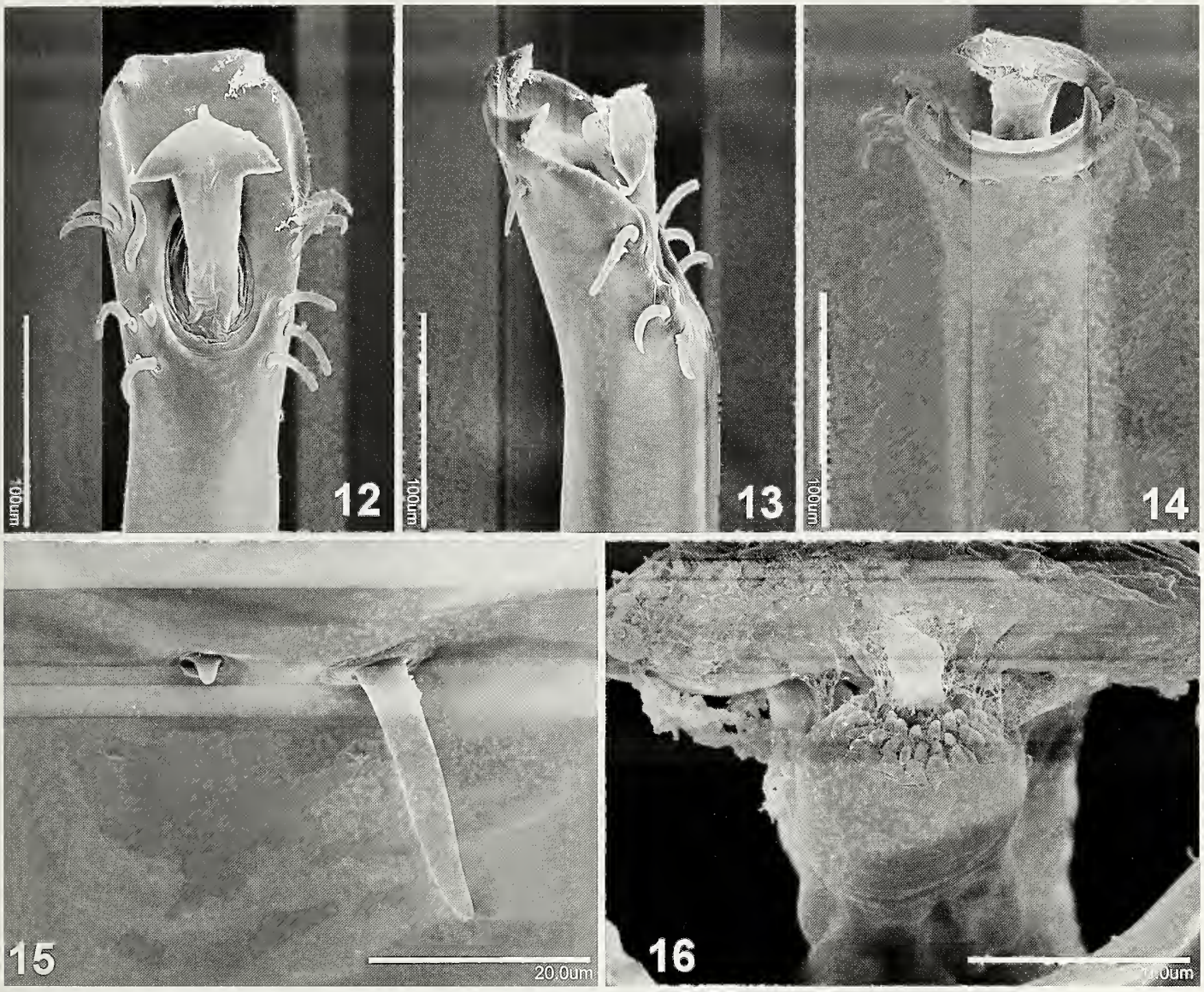
Figures 8–11.—*Philora tuxtlae* Goodnight & Goodnight 1954, male. 8. Pedipalp ectal view (arrow points to setiferous tubercle on pedipalpal tibia); 9. Pedipalp mesal view; 10. Chelicera ectal view; 11. Chelicera frontal view.

composed by 2 low and contiguous teeth; movable finger with medial concavity (Figs. 10, 11).

Pedipalp: Coxa with median irregular row of tubercles. Trochanter globular, with 2 prominent spiniform tubercles ventrally. Femur slightly concave mesally, with few spiniform tubercles dorsally; ventrally with 3 noticeable, spiniform tubercles, 2 basal, the basalmost larger than the others; the third one distally displaced. Patella unarmed, covered only by setae. Tibia and tarsus with 3 spiniform tubercles on both sides, the bases of theses tubercles are conical, with the setae displaced basally (Figs. 8, 9).

Legs: Measurements: I: 0.35/0.20/0.70/0.55, II: 1.00/0.36/0.85/0.85, III: 0.45/0.25/0.69/0.80, IV: 1.00/0.35/0.70/1.00. All legs similar in ornamentation, covered by small setae, denser distally; posterior legs without remarkable sexual dimorphism, covered by small setae, denser distally. Metatarsus IV with dorsodistal tubercle, small and inconspicuous, with a small, curved apical seta (Figs. 4–7, 44).

Genitalia: Setae of pars distalis filiform, rounded apically, without grooves; grouped into 2 distinct sets, 1 basal and 1 mesal, of 3 setae each. Ventroapical region of pars distalis with 2 submedial microsetae and 2 lateral macrosetae pointing basally, similar to the others setae of pars distalis; ventroapical margin with 2 pointed apices. Base of follis excavated; bilobular dorsal projections of the follis contiguous with it, apices robust, pointed distally. Stylus short and hidden within



Figures 12–16.—*Philora tuxtlae* Goodnight & Goodnight 1954, male genitalia. 12. Dorsal view; 13. Lateral view; 14. Dorso-ventral view; 15. Detail of one ventroapical microsetae and one ventroapical macrosetae on pars distalis; 16. Dorsal view of bilobular projection of follis.

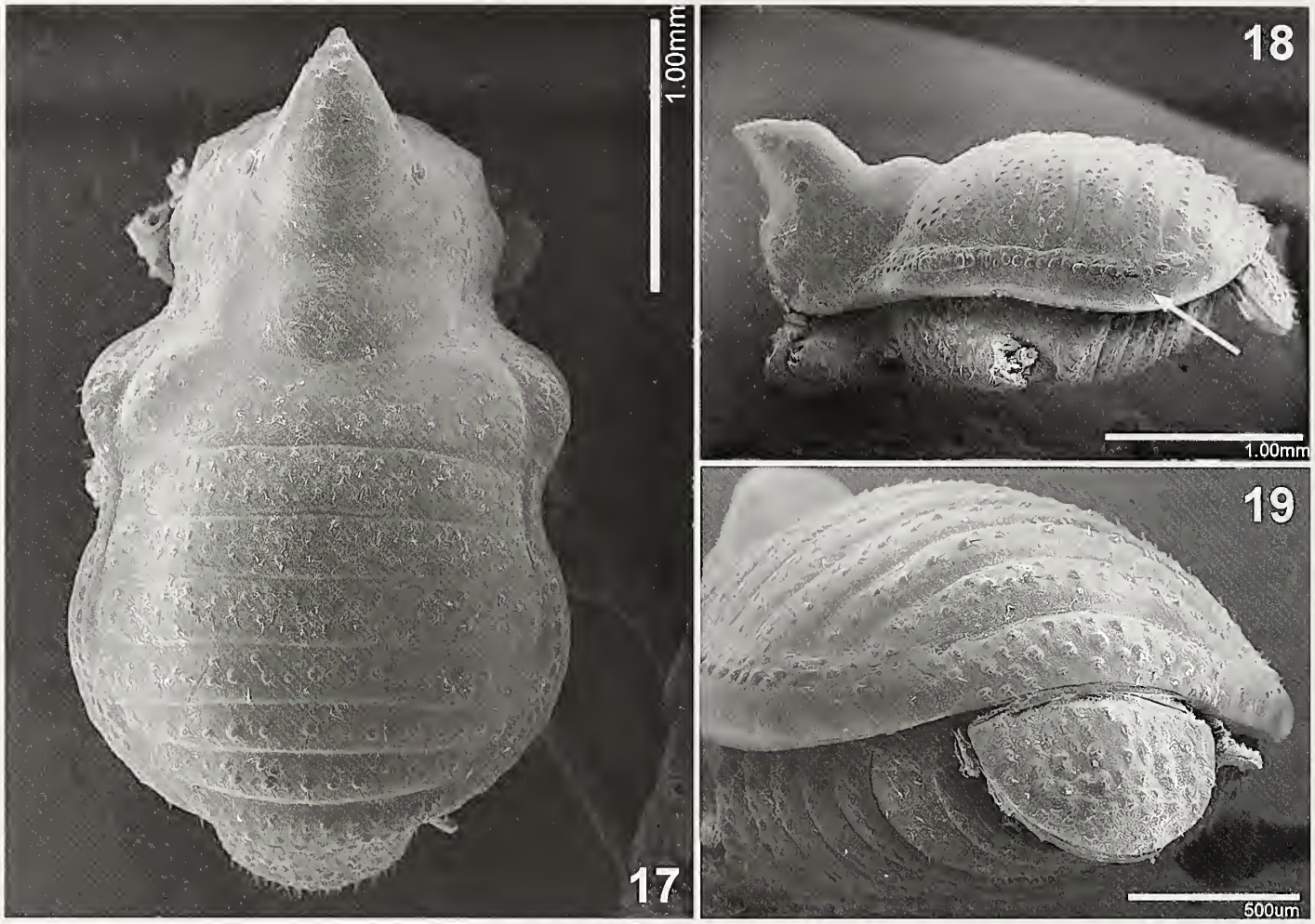
the apical portion of follis, spiniform projections only visible on the ventral side of glans. (Figs. 12–16).

Color: Scutum and venter dark brown, boundaries between dorsal areas lighter. Lateral margins of scutum and anterior portion of dorsal areas slightly darker. Ocularium and prosoma reticulated, background color brown, with black grid. Chelicera and pedipalps are very similar in coloration to ocularium, but lighter. Legs light brown, distal articles dark yellow. Stigmatic area with four light-colored pointed areas, almost white (Figs. 35, 36).

Female: Very similar to male, differing only in slightly larger size, and the shape and coloration of the stigmatic region. Females with lateral margins of stigmatic area shorter than on males, without 4 light-colored areas ventrally (Figs. 37, 38).

Variation: There is minimal morphological variation among males and females; the following variation in size was observed [ranges in mm (males/females) n = 10]: scutum length 2.3–2.5/2.5–2.7, pedipalpal femur length 0.6–0.7/0.7–0.8, femur II length 1.0–1.1/1.1–1.2, femur IV length 1.2–1.4/1.2–1.3.

Remarks.—The type material of this species was not studied, but we consider that the material examined corresponds to *P. tuxtlae* because in the original description the authors mentioned the following characters: small size, low tarsal count, dorsal ornamentation; which match the specimens redescribed here. Further, the material examined comes from localities within the "Reserva Especial de la Biosfera del Volcán San Martín", which includes the type locality (Fig. 53). We question the sex of the types, as indicated by the original authors, because males and females are very similar and we have examined some stygnopsids of the genera *Hoplobunus* Banks 1900, *Karos* Goodnight & Goodnight 1944 and *Paramitraceras*, which were identified and labeled by Goodnight and Goodnight, and in most of them the sexual and life-stages (adult vs. juvenile) determinations are erroneous. These errors in determining the sex by the Goodnights



Figures 17–19.—*Philora quetzalzin* new species, male. 17. Habitus dorsal view; 18. Habitus lateral view (arrow points to posterior lateral light-colored areas); 19. Habitus dorso-posterior view.

have been corroborated by other authors (e. g., Vázquez & Cokendolpher 1997; Cokendolpher 2004; Shear, 2010; Cruz-López & Francke 2013), and thus we do not trust their determinations without examining the types.

Distribution.—*Philora tuxtlae* is only known from the tropical rainforest of the Reserva Especial de la Biósfera, Volcan San Martín, Los Tuxtlas, Veracruz (Fig. 53).

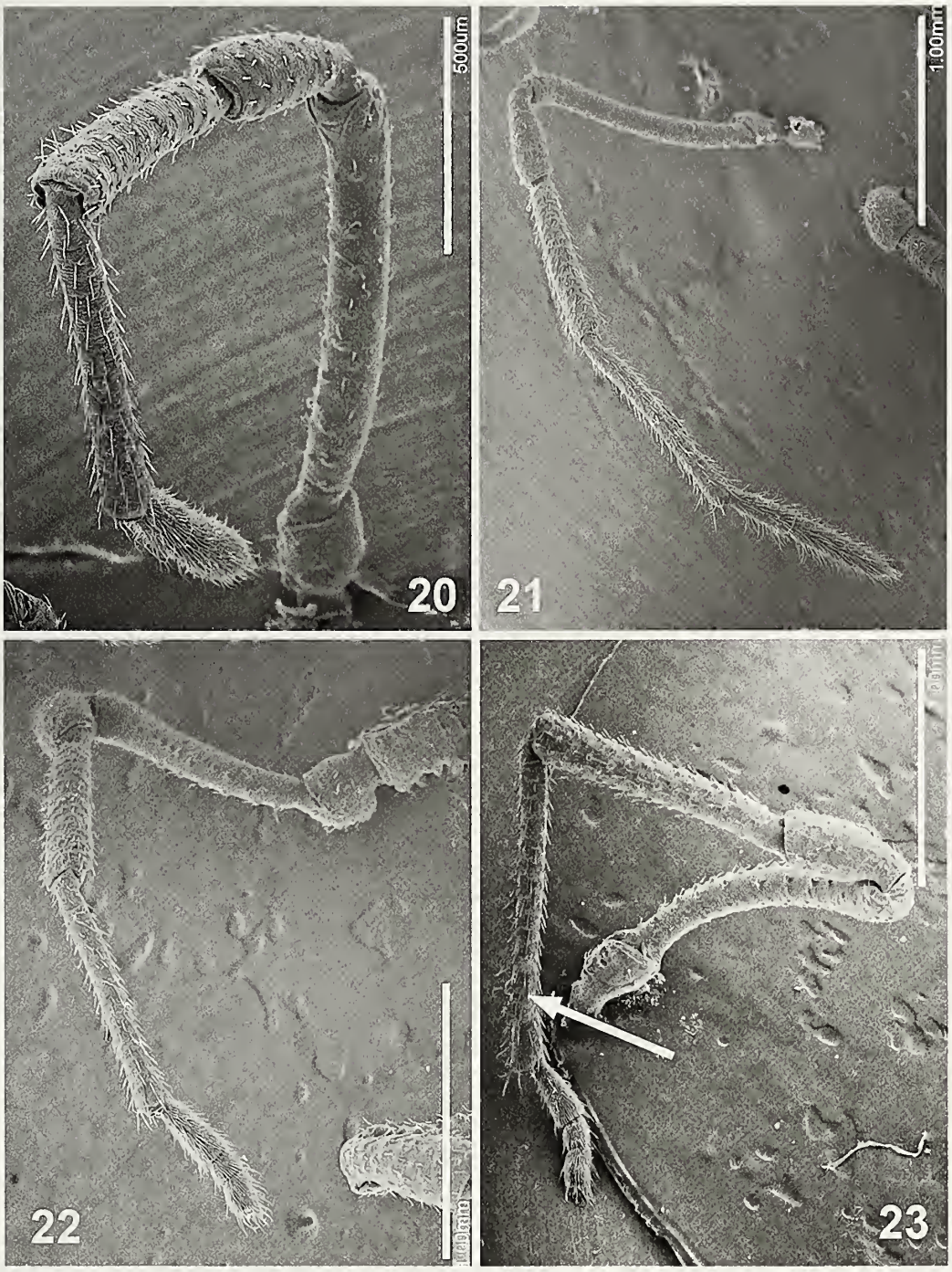
Natural history.—The specimens collected in August 2005 and January 2012 were located by actively searching in appropiate microhabitats and were found inside decomposing tree stumps. Using this collecting method we also found many laniatorean specimens of the genera *Flaccus* Goodnight & Goodnight 1947 of the family Biantidae Thorell 1889 [we decided not to follow the synonymy of *Flaccus* under *Styguomma* Roewer 1912, proposed by Goodnight & Goodnight (1951), according to unpublished data of Pérez-González (2006)]; *"Cyuorta"* Koch 1839 (Kury et al. 2007), *Ergiuulus* Roewer 1912, *Eucynortula* Roewer 1912, and *Paecilaema* Koch 1839 of the family Cosmetidae Koch 1839; *Hoplobuuus*, *Paranitraceras*, and an undetermined genus of the family Stygnopsidae; and *Pachylicus* Roewer 1923 of the family Zalmoxidae Sorensen 1886. However, active searching was a poor method to collect *Philora* specimens. In November 2012, we collected by sifting leaf litter over a white sheet, obtaining contrasting results, and many more specimens of *Philora* were collected. This species showed thanatosic behavior, remaining stationary for several minutes, and resembling small pieces of dirt on the white sheet (making visual search difficult). However, after a few minutes, they started crawling away and their identification and capture became much easier. *Philora tuxtlae* was found in both well-preserved and disturbed rainforest (mostly cleared to make pastures for cattle) where there was leaf-litter accumulation.

Philora quetzalzin new species
(Figs. 17–32, 33, 35, 39, 40, 45, 46)

Type material.—MEXICO: *Veracruz*, holotype male, 5 km E of Tlaquilpa, Municipio Tlaquilpa (18°38′30.228″N, 97°06′26.495″W, 2,233 m), 22 January 2010, O. Francke, A. Valdez, C. Santibañez, J. Cruz (CNAN-T0743). Paratypes: 1 male, same data as holotype (CNAN-T0744); 1 male, 1 female, same locality, 23 March 2007, O. Francke, A. Valdez, C. Santibañez, A. Ballesteros, H. Montaño (CNAN-T0745).

Etymology.—The specific name is derived from "quetzalzin", which in Nahuatl means "small beauty". The name is used as a noun in apposition.

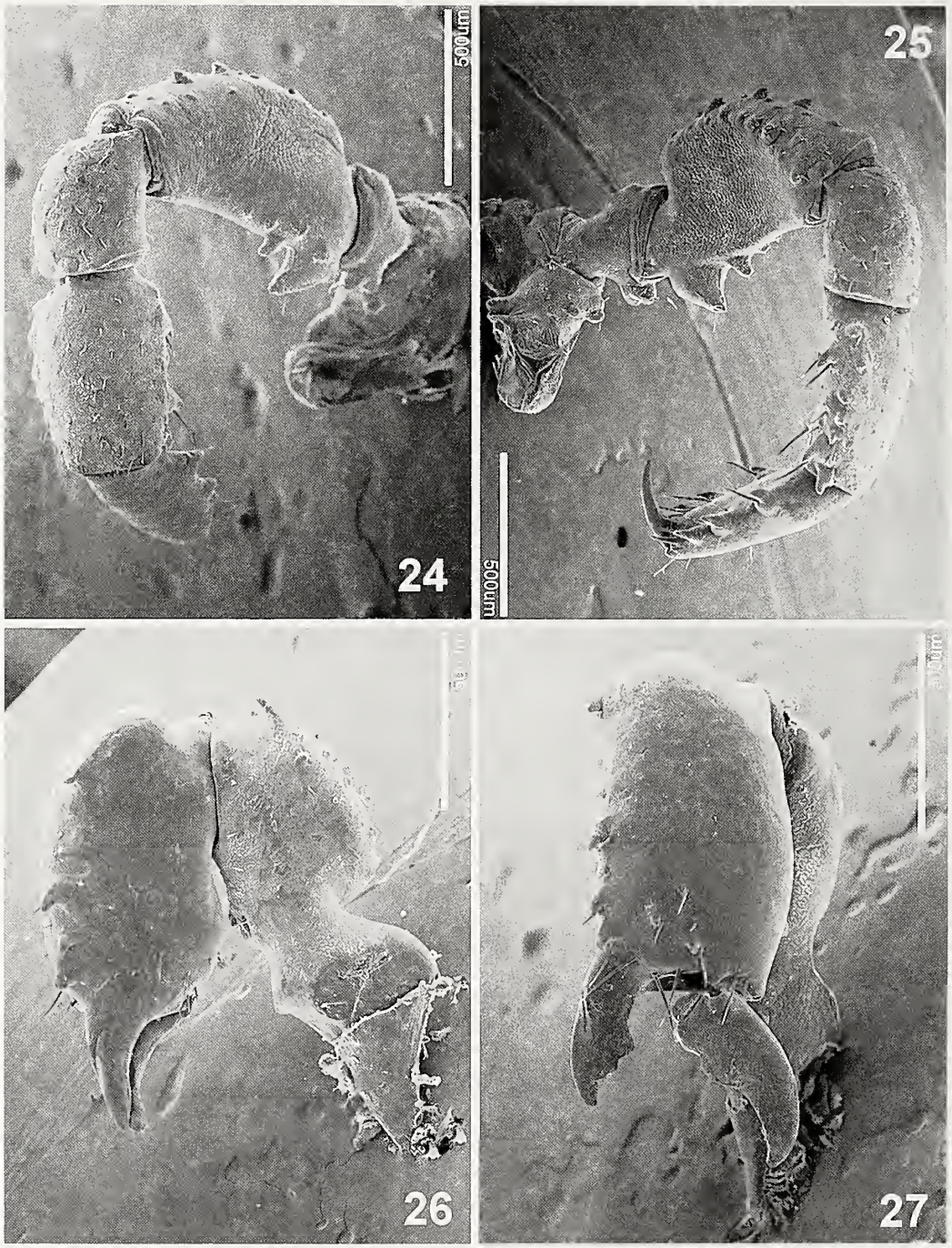
Diagnosis.—*Philora quetzalzin* differs from *P. tuxtlae* in having a moderately dense, noticeable dorsal ornamentation; a



Figures 20–23.—*Philora quetzalzin* new species, male. 20. Leg I frontal mesal view; 21. Leg II mesal view; 22. Leg III mesal view; 23. Leg IV mesal view (arrow points to dorsodistal setiferous tubercle).

strong ocularium with a marked posterior bulge; and tubercles of posterior tergites similar in size and shape to those on the dorsum (Figs. 17–19, 33, 34). It exhibits notable sexual dimorphism, with males having a strongly developed cheliceral hand (scutum/ehelieeral hand ratio: 2.8 in males, vs. scutum/cheliceral hand ratio: 3.1 in females), and the base of the ocularium is wider in males than in females; whereas in *P. tuxtlae* there is almost no sexual dimorphism. The two species also differ in cheliceral dentition: the fixed finger has 2 teeth in *P. tuxtlae* and 3 teeth in *P. quetzalzin*; the movable finger has no teeth in *P. tuxtlae* and 2 teeth in *P. quetzalzin* (Figs. 10, 11, 26, 27). The dorsal tubercle on metatarsus IV is distinctive and meso-distal (Figs. 23, 46), whereas on *P. tuxtlae* it is inconspicuous and distal. The setae of the pars distalis number 10 pairs, are disorganized in the basal portion, originating basally to the follis, with medial grooves, and are distally pointed rather than rounded. The ventroapical macrosetae are considerably swollen and quite distinctive (Figs. 28–32).

Description.—*Male (holotype):* Measurements: Scutum length: 2.9, scutum width: 1.9. Dorsum: scutum densely covered with small, rounded setiferous tubercles, slightly larger posteriorly. Prosoma rugose. Base of ocularium broad,



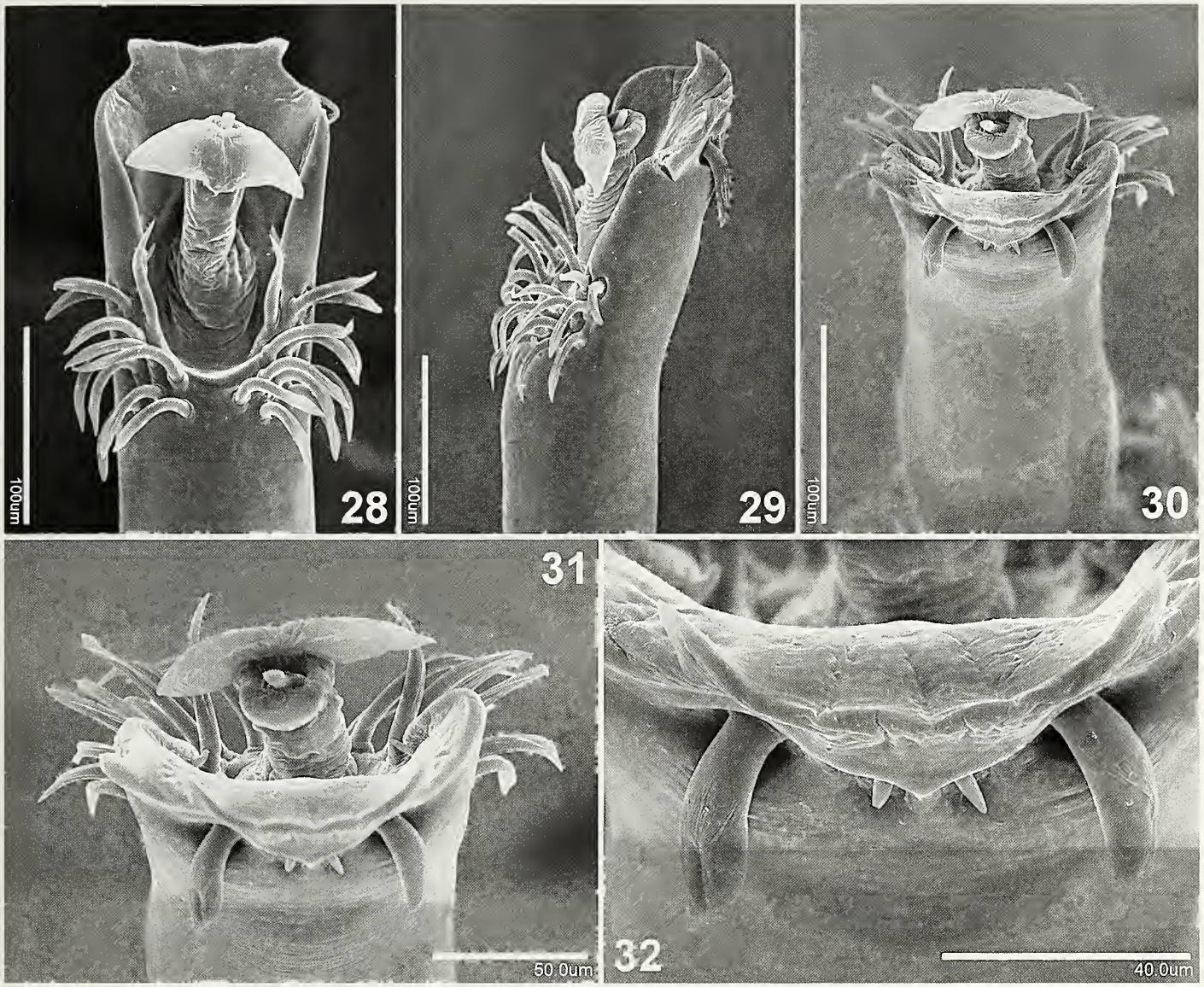
Figures 24–27.—*Phiłora quetzalzin* new species, male. 24. Pedipalp frontal ectal view; 25. Pedipalp mesal view; 26. Chelicera ectal view; 27. Chelicera frontal view.

occupying over half of prosoma, dorsally covered with anteriorly directed small tubercles, apex of ocularium robust, ocularium with prominent posterior bulge (Figs. 17–19).

Venter: Uniformly ornate with small setiferous tubercles, smaller than on dorsum, except in coxa I where the tubercles are spiniform and slightly developed. Stigmatic area with lateral margins straight, short. Posterior light-colored pointed areas somewhat fused (Fig. 39). Free sternites covered by small setiferous tubercles.

Chelicera: Cheliceral hand swollen (scutum/cheliceral hand ratio: 2.8). Basichelicerite covered dorsally by spiniform tubercles, the largest on meso-distal face. Cheliceral hand inserted dorsally on the basichelicerite; in frontal view covered with 3 spiniform tubercles distally pointed. Cheliceral dentition heterogeneous: fixed finger with 3 teeth, the basal most slightly larger; movable finger with 2 teeth, bulge-shaped, rounded (Figs. 26, 27).

Pedipalp: Coxa with median irregular row of setiferous tubercles. Trochanter globular with two blunt, larger spiniform tubercles. Femur concave on mesal side, with 2 irregular rows of spiniform setiferous tubercles ventrally; mesal row with 2 large tubercles, basal most largest; ectal row with 4



Figures 28–32.—*Philora quetzalzin* new species, male genitalia. 28. Dorsal view; 29. Lateral view; 30. Dorso-ventral view; 31. Dorsal view of bilobular projection of glans; 32. Details of ventroapical pairs of micro- and macrosetae on pars distalis.

smaller ones. Femur covered dorsally by 2 rows of small spiniform tubercles, increasing in size distally. Patella unarmed, covered only by setae. Tibia with 3 setiferous spiniform tubercles on each margin. Tarsal armature similar to tibia, setiferous tubercles with the setae at the base (Figs. 24, 25).

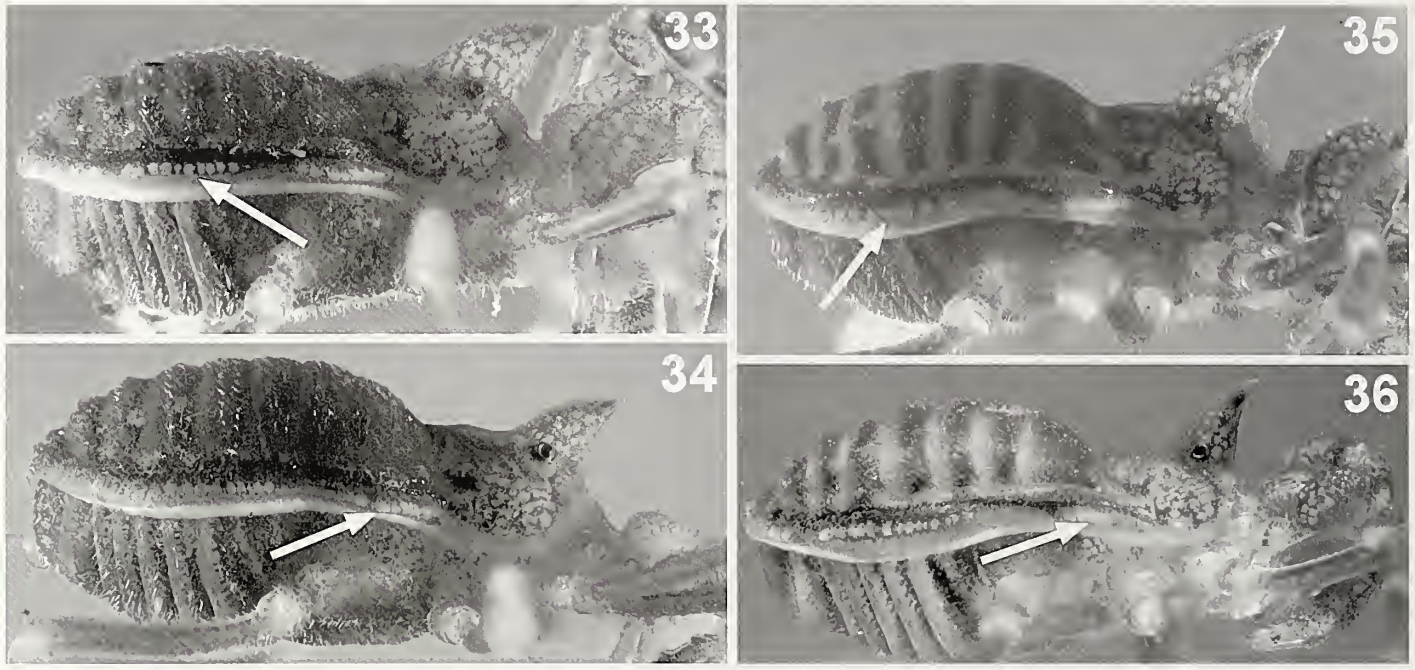
Legs: Measurements: I: 0.55/0.40/0.95/0.75, II: 1.40/0.55/1.05/1.00, III: 0.65/0.40/0.80/1.00, IV: 1.25/0.45/0.90/1.25. All legs similar in ornamentation, covered by numerous small setae. Femora III and IV curved. Leg IV without sexually dimorphic ornamentation. Metatarsus IV with strong spiniform setiferous tubercle mesodistally, with 1 or 2 apical setae (Figs. 20–23, 46).

Genitalia: Pars distalis with 10 pairs of setae, basal to follis, without distinct groupings, all setae with distal median groove. Lateral margins of pars distalis in dorsal view curved towards the follis, with a pair of minute setae on the lateral margins hidden by curls. Apex of distal ventroapical margin with two small lateral projections. Two pairs of ventroapical setae, the middle pair formed by two microsetae, very close between them; the lateral setae slightly spoon-shaped distally, with an apical median groove. Follis narrower than the maximum width of pars distalis, base of follis excavate; bilobular dorsal projection widespread, apices rounded distally; stylus short and hidden within the apical portion of follis. Spiniform projections small and only present in the ventral side of apical follis (Figs. 28–32).

Color: Similar to *P. tuxtlae*, but the boundaries between dorsal areas of scutum almost as dark as the rest of dorsum (Figs. 33, 34).

Female (paratype): Differs from the male in having a narrower ocularium, chelicera noticeably smaller (scutum/cheliceral hand ratio: 3.1), setiferous tubercles of pedipalps less developed and having lateral margins of stigmatic area shorter than the males (Figs. 33, 34, 39, 40).

Distribution.—This species is known only from the type locality (Fig. 53).



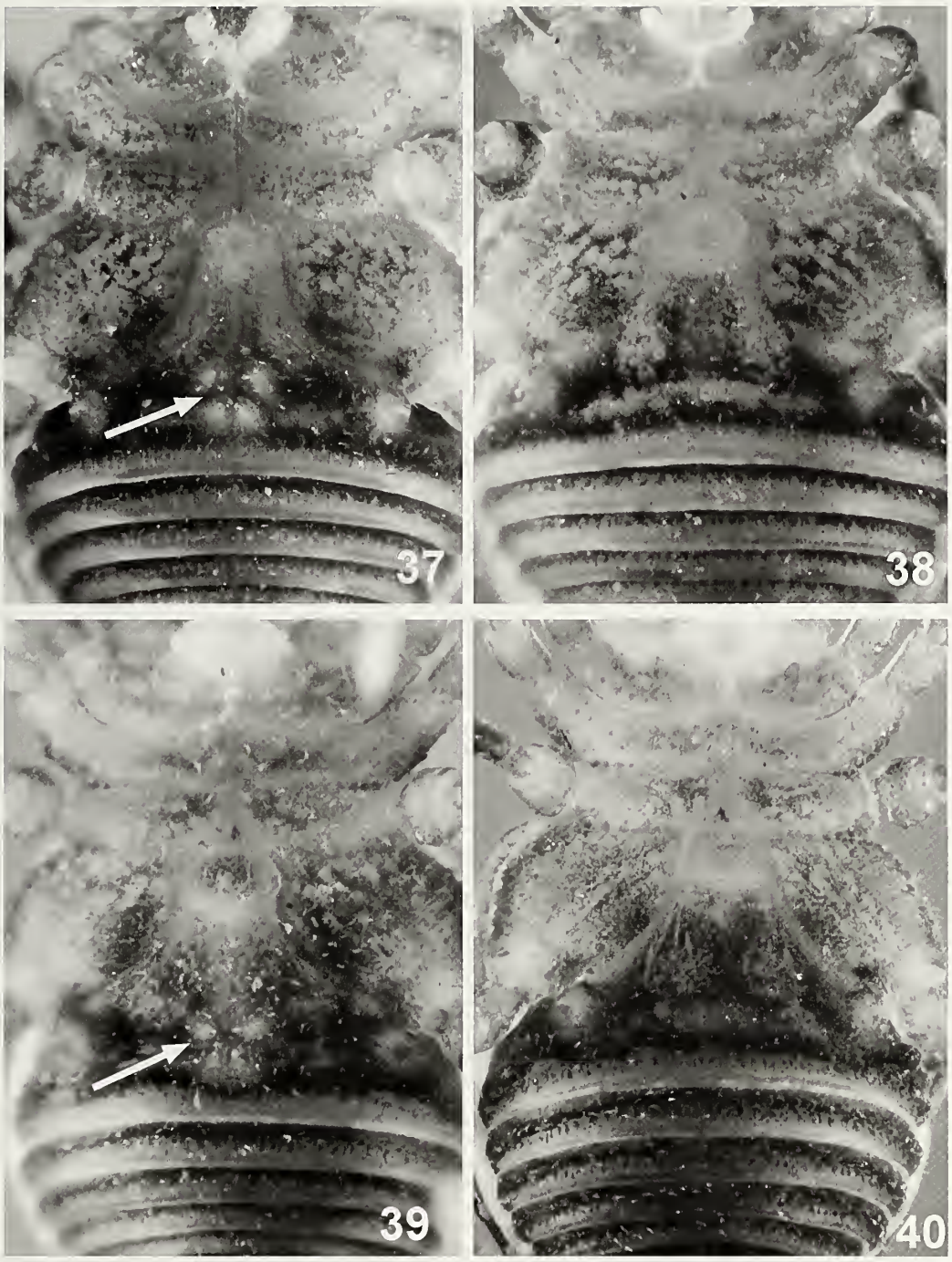
Figures 33–36.—*Philora* species, male and female lateral view. 33. *Philora quetzalzin* new species, male; 34. *P. quetzalzin*, female; 35. *P. tuxtlae* Goodnight & Goodnight 1954, male; 36. *P. tuxtlae* female. Arrows indicate anterior (females, lower illustrations) and posterior (males, upper illustrations) light-colored areas.

Natural history.—Similar to *P. tuxtlae*, the speeimens collected in 2010 showed thanatosic behavior, and were found among the roots of decomposing tree stumps, forming a small aggregation with specimens of *Flaccus* sp. *Philora quetzalzin* inhabits a pine-oak forest, above 2,000 m, unlike *P. tuxtlae* whieh lives in the rainforest of Los Tuxtlas region at a lower altitude of less than 1,200 m.

DISCUSSION

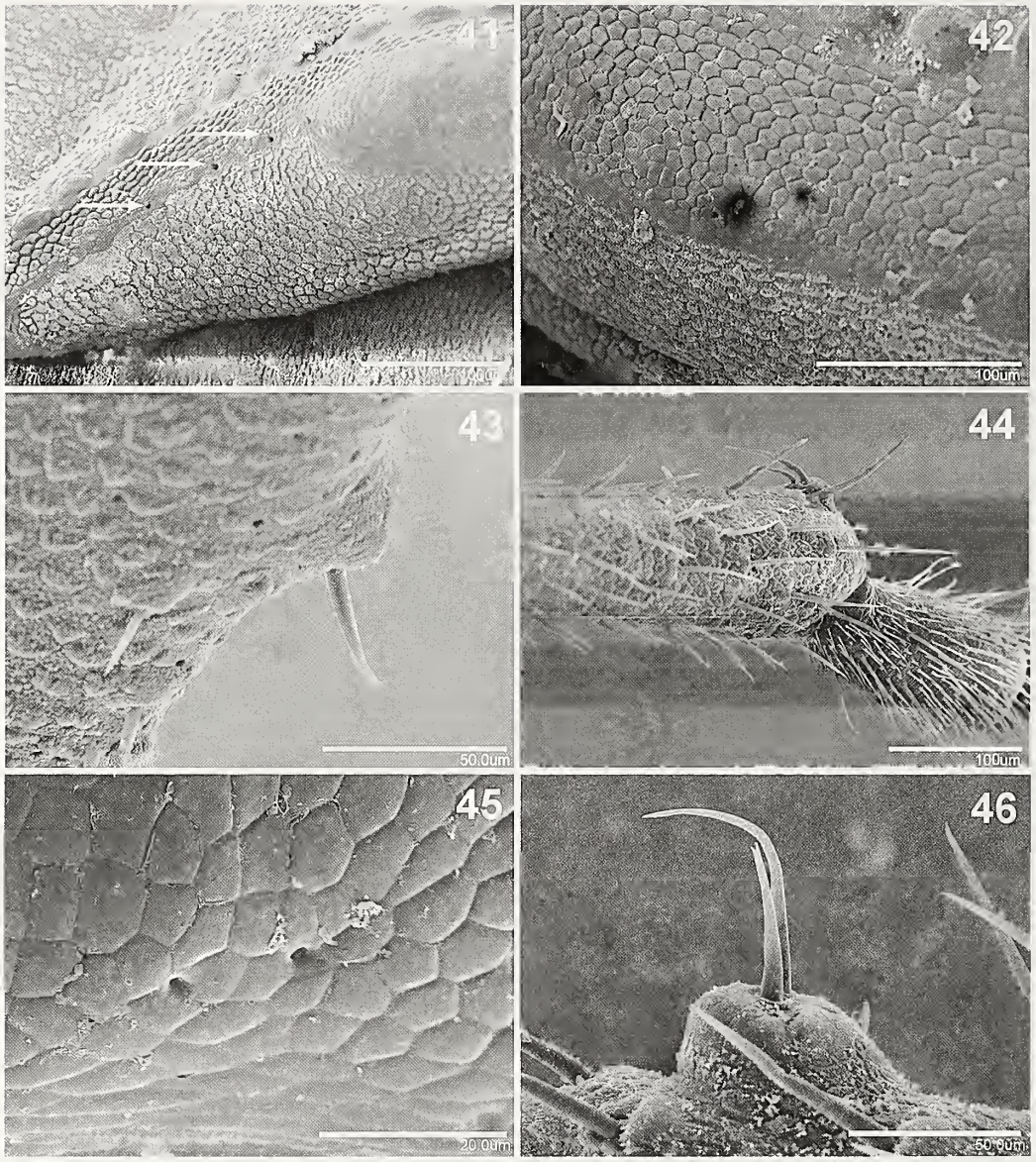
Goodnight & Goodnight (1954) argued that tarsal counts alone were sufficient to differentiate the genus *Philora* from its close relative *Paramitraceras*. It is surprising that those authors did not mention the presence of a scutum completum in the generie diagnosis of *Philora*, because this character is quite distinctive. The fusion of all dorsal tergites forming a scutum completum was previously known only in the suborder Cyphophthalmi Simon 1879; in the families Dicranolasmatidae Simon 1879, Nemastomatidae Simon 1872 and Trogulidae Sundevall 1833 within the suborder Dyspnoi Hansen & Sorensen 1904 (Shear 2006; Sharma & Giribet 2011). Regarding the suborder Laniatores, the scutum completum is present in the family Sandokanidae Özdikmen & Kury 2007 (formerly Oncopodidae Thorell 1876), in the males of *Heteropachylus inexpectabilis* (Soares & Soares 1946) of the family Gonyleptidae Sundevall 1833, and presumably in *Paralola buresi* Kratochvíl 1951 of the family Phalangodidae Simon 1879 (Schwendinger 2007; Ubick 2007; Mendes 2011). This morphological condition was considered plesiomorphic in the order, but this hypothesis is inconsistent with recent outgroup comparison and with the retention of primitive dorsal longitudinal muscles in higher Opiliones (Shultz & Pinto-da-Rocha 2007); and the scutum completum appears to have evolved convergently in several Opiliones lineages (Sharma & Giribet 2009). Moreover, reciprocally in Cyphophthalmi, Sandokanidae and *Philora*, this character is matched by low tarsal counts and could reflect adaptations to similar ecological niches, but this hypothesis has not been tested (Sharma & Giribet 2009, 2011). The recent hypothesis of phylogenetic relationships, using molecular data, of the families with all or one member with scutum completum is: the family Sandokanidae is considered the sister group of the non-phalangodid Grassatores Kury 2002, whereas the family Stygnopsidae is considered the sister group of the superfamily Gonyleptoidea; and finally, the family Gonyleptidae is within the Gonyleptoidea (Giribet et al. 2010; Sharma & Giribet 2011).

The phylogenetic and taxonomic status of Gonyleptidae and Sandokanidae has been well studied, wherein the external morphology and the male genitalia of the majority of the genera and species of the family are well known (e.g., Schwendinger & Martens 2002; Schwendinger 2006, 2007; DaSilva & Gnaspini 2009; Yamaguti & Pinto-da-Rocha 2009; DaSilva & Pinto-da-Rocha 2010; Mendes 2011). In contrast, within the family Stygnopsidae, external morphology and male genitalia are well known for the genera *Chinquipellobunus* Goodnight & Goodnight 1944 (Cokendolpher 2004) and five of six species of *Paramitraceras* (Cruz-López & Francke 2012, 2013). There are published drawings of the male genitalia of the *Hoplobunus boneti* (Goodnight & Goodnight 1942), *H. queretarius* Šilhavý 1974, *Karos rugosus* Goodnight & Goodnight 1971, *Mexotroglinus sbordonii* Šilhavý 1977, *Sbordonia arnigera*, both known species of the genus *Stygnopsis* Sorensen 1902, both known species of the genus *Troglostygnopsis* Šilhavý 1974, and SEM photos of *Karos* sp. and *Stygnopsis valida* (Sørensen 1884) (Šilhavý 1974, 1977; Mendes & Kury 2007). Mendes & Kury (2007) described the male genitalia of the family Stygnopsidae, but in the majority of species the male genitalia are unknown.



Figures 37–40.—*Philora* species, male and female ventral views. 37. *Philora tuxtlae* Goodnight & Goodnight 1954, male; 38. *P. tuxtlae* female; 39. *Philora quetzalzin* new species, male; 40. *P. quetzalzin* female. Arrows indicate the four ventral light-colored pointed areas on the males of *Philora* species.

We have observed the male genitalia of some stygnopsids using a scanning electronic microscope and have noted that the male genitalia of the type species of *Troglostygnopsis*, along with the known male genitalia of the genera *Paramitraceras*, *Philora*, and presumably the genus *Sbordonia* (based on the drawing by Šilhavý 1977), share a similar and unique genital pattern, herein called the Paramitraceras-pattern. This pattern is recognizable by having 1) setae of pars distalis generally forming two rows or groups, one dorsolaterally or mesal, and the other, laterobasal and ventrally; 2) numerous pairs of setae in these two rows, from three to fourteen pairs; 3) pars distalis very wide, follis narrow compared with it; 4) presence of a bilobular dorsal projection of the follis; and 5) presence of a unique pair of micro-ventral setae in the meso or meso-distal region of ventral plate (Figs. 47–52). Regarding the other described species of *Troglostygnopsis*, *T. inops* (Goodnight & Goodnight 1971), we have observed that it does not share this male genitalic pattern, and possibly this species should be transferred out of the genus. A phylogenetic analysis of these and other stygnopsid genera would clarify



Figures 41–46.—*Philora* species, details of lateral pores, setiferous tubercle of pedipalp and dorsal distal tubercles of femur IV; 41. *Philora tuxtlae* Goodnight & Goodnight 1954, male, antero-lateral pores (arrows, see also arrow in Figure 2); 42. *P. tuxtlae* male, detail of a pore; 43. *P. tuxtlae* male, setiferous tubercle of pedipalpal tibia (see arrow in Figure 8); 44. *P. tuxtlae* male, detail of dorsal distal spiniform setiferous tubercle on metatarsus IV (see arrow in Figure 7); 45. *Philora quetzalzin* new species, details of latero-posterior pores (arrow in Figure 18); 46. *P. quetzalzin*, detail of dorso meso-distal spiniform setiferous tubercle on metatarsus IV (see arrow in Figure 23).

whether this pattern is due to common ancestry or due to homoplasy. Those three genera can be differentiated by combinations of external and genital characters (Table 1).

The "lateral projections" (Šilhavý 1974, 1977) are present in both species of the genus *Philora*; these structures and the light-colored lateral areas on the sides of the scutum were observed under SEM, and there are numerous micropores in those areas (Figs. 33–36, 41, 42, 45). Šilhavý (1974) proposed that these lateral projections, present in the stygnopsid genera *Karos*, *Parauuitraceras*, *Sbordouia* and *Troglostygnopsis* could be glandular openings similar to those reported on other Laniatores (Eisner et al. 2004; Machado et al. 2005; Willemart et al. 2010). A detailed examination using SEM of these light-colored areas on those other genera will contribute to a better knowledge about glandular openings in the family Stygnopsidae.

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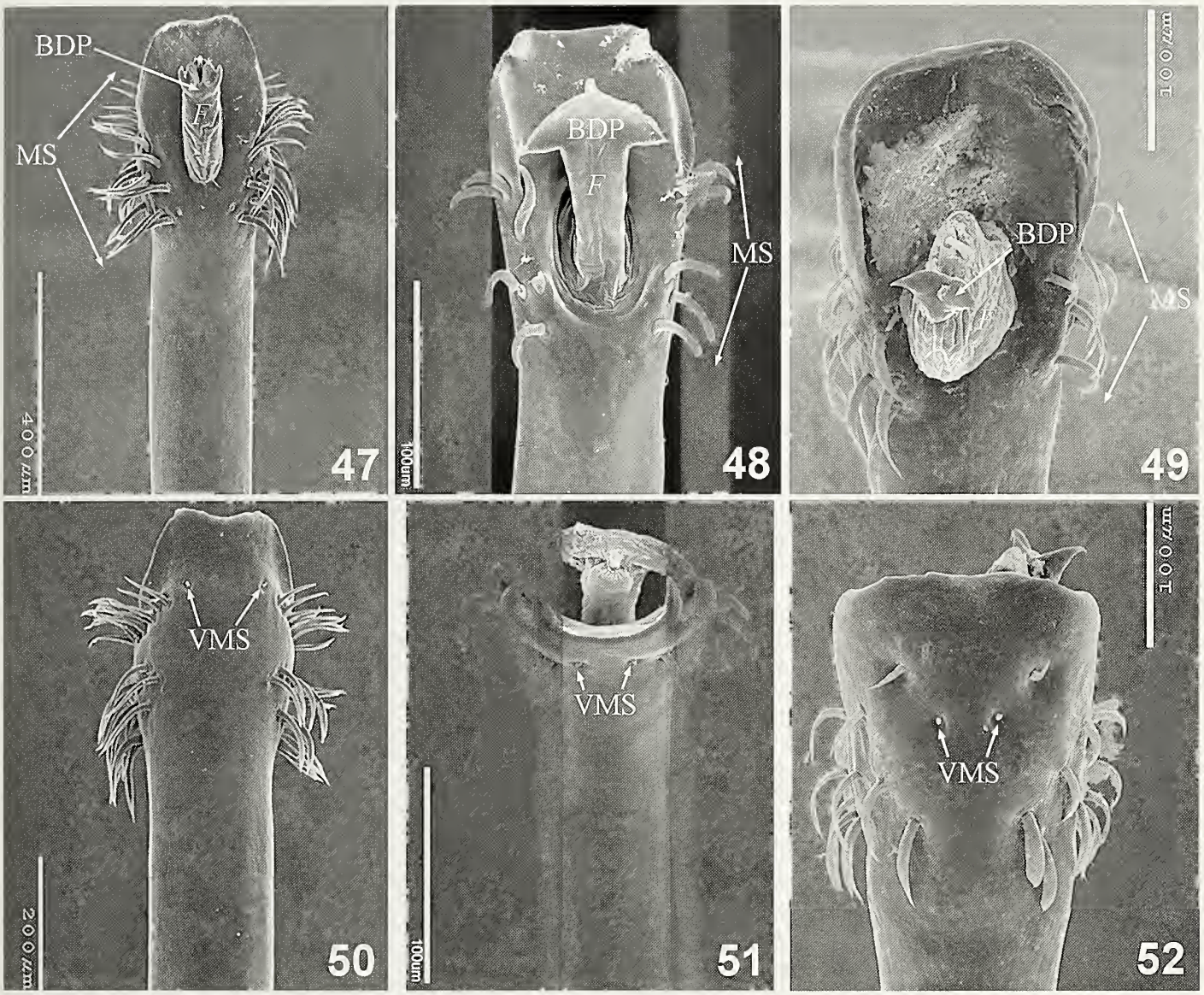

Figures 47–52.—Male genitalia of the genera having the Paramitraceras-pattern. 47 & 50. *Paramitraceras granulatum* Pickard-Cambridge 1905; 47. Dorsal view; 50. Ventral view. 48 & 51. *Philora tuxtlae* Goodnight & Goodnight 1954; 48. Dorsal view; 51. Ventral view. 49 & 52. *Troglostygnopsis anophthalma* Šilhavý 1974; 49. Dorsal view; 52. Ventral view. Abbreviations: BDP = bilobular dorsal projection, *F* = follis, MS = macrosetae, VMS = ventral microsetae.

LITERATURE CITED

Cokendolpher, J.C. 2004. Revalidation of the harvestman genus *Chinquipellobunus* (Opiliones: Stygnopsidae). Texas Memorial Museum, Speleological Monographs 6:143–152.

Cruz-López, J.A. & O.F. Francke. 2012. Una nueva especie del género *Paramitraceras* Pickard-Cambridge (Opiliones: Laniatores: Stygnopsidae) de Veracruz, México. Revista Ibérica de Aracnología 20:17–23.

Cruz-López, J.A. & O.F. Francke. 2013. Two new species of the genus *Paramitraceras* Pickard-Cambridge, 1905 (Opiliones: Laniatores: Stygnopsidae). Zootaxa 3641:481–490.

DaSilva, M.B. & P. Gnaspini. 2009. A systematic revision of Goniosomatinae (Arachnida: Opiliones: Gonyleptidae), with a cladistic analysis and biogeographical notes. Invertebrate Systematics 23:530–624.

DaSilva, M.B. & R. Pinto-da-Rocha. 2010. Systematic review and cladistic analysis of the Hernandariinae (Opiliones: Gonyleptidae). Zoologia 27:577–642.

Eisner, T., C. Rossini, A. González & M. Eisner. 2004. Chemical defense of an opilionid (*Acanthopachylus aculeatus*). Journal of Experimental Biology 207:1313–1321.

Giribet, G., L. Vogt, A. Pérez-González, P. Sharma & A.B. Kury. 2009. A multilocus approach to harvestman (Arachnida: Opiliones) phylogeny with emphasis on biogeography and the systematics of Laniatores. Cladistics 26:408–437.

Goodnight, C.J. & M.L. Goodnight. 1951. The genus *Stygnomma* (Phalangida). American Museum Novitates 1491:1–20.

Goodnight, C.J. & M.L. Goodnight. 1954. The opilionid fauna of an isolated volcano in Southeastern Veracruz. Transactions of the American Microscopical Society 73:344–350.

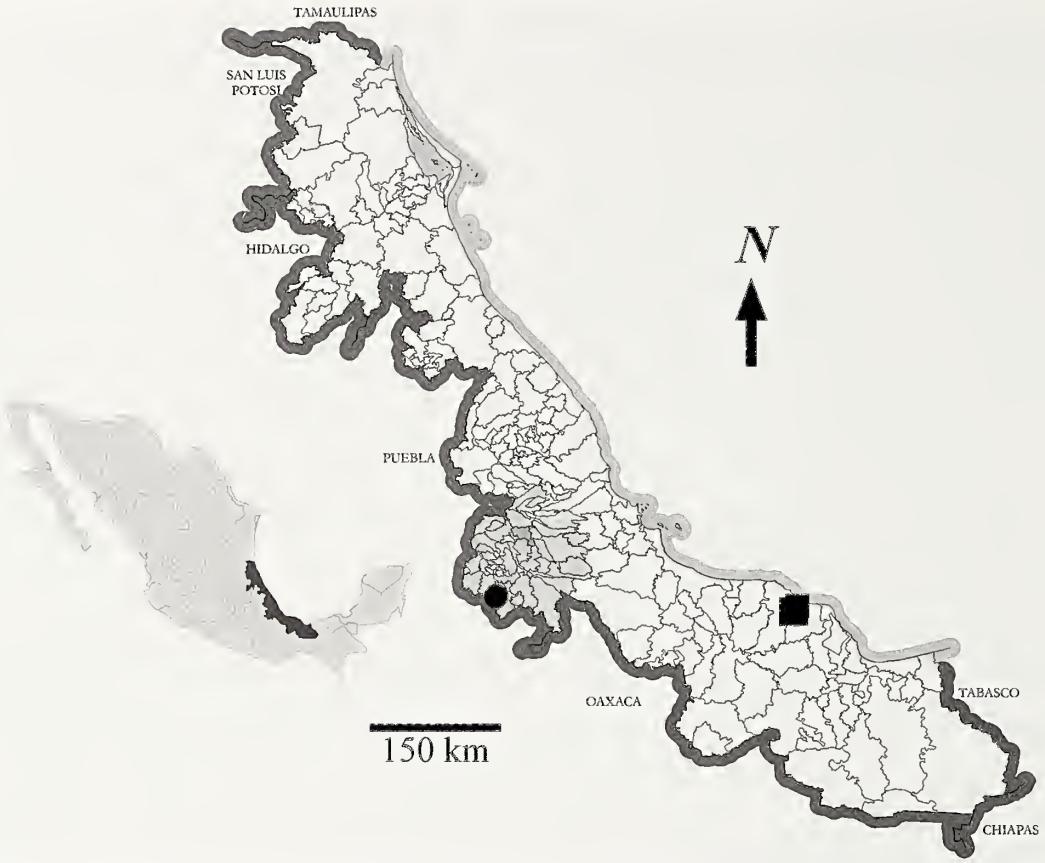

Figure 53.—Distribution of the species of *Philora*. State of Veracruz enlarged. Circle: *Philora quetzalzin* new species. Squares: *Philora tuxtlae* Goodnight & Goodnight 1945, including the type locality.

Table 1.—Differences in morphological characters between the stygnopsid genera *Paramitraceras* Pickard-Cambridge 1905, *Philora* Goodnight & Goodnight 1954, *Sbordonia* Šilhavý 1977, and *Troglostygnopsis anophthalma* Šilhavý 1974.

	Paramitraceras	*Philora*	*Sbordonia*	*T. anophthalma*
Scutum	*magnum*	*completum*	*magnum*	*magnum*
Eyes	Present	Present	Present	Absent
Body, lateral view	Opisthosoma convex	Opisthosoma convex	Opisthosoma convex	Opisthosoma flattened
Pedipalpal armature	Absent	Present	Present	Present
Pedipalpal armature on the tibia	-	Entire length	Distally only	Entire length
Setae and base of setiferous tubercles of the pedipalpi	-	Not contiguous	Contiguous	Contiguous
Length of the setiferous tubercles of pedipalpi	-	Not greater than respective segments	Not greater than respective segments	Greater than respective segments
Ventral armature of the femur IV	*P. femorale* only with a basal ventro-distal bulge	Absent	With conspicuous spiniform tubercles	Absent
Lenght of femur IV	Less than or equal to scutum	Less than or equal to scutum	Less than or equal to scutum	Longer than scutum
Distitarsus I and II	2/2–3	1/1	2/2	3/3
Origin of lateral setaes of pars distalis	Lateral to follis	Basal and lateral to follis	unknown	Lateral to follis
Ventral microsetae	Distant from each other	Close between them	unknown	Close between them
Position of the ventral microsetae respect to apical pair of dorsal lateral setae row	At the same level or slightly apical	Basal to them	unknown	Basal to them
Apical pair of the dorsal lateral setae row	Contiguous with the rest	Separated from the rest, close to ventral microsetae	unknown	Separated from the rest, close to ventral microsetae

Kury, A.B. 2003. Annotated catalogue of the Laniatores of the New World (Arachnida, Opiliones). Revista Ibérica de Aracnología. Vol. Especial monográfico 1.

Kury, A.B. 2011. Order Opiliones Sundevall, 1833. *In* Zhang, Z.-Q. (ed.). Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. Zootaxa 3148:112–114.

Kury, A.B. 2012. First report of the male of *Zamora granulata* Roewer, 1928, with implications on the higher taxonomy of the Zamorinae Kury, 1997 (Opiliones, Laniatores, Cranaidae). Zootaxa 3546:29–42.

Kury, A.B. & J.C. Cokendolpher. 2000. Opiliones. Pp. 137–157. *In* Llorente-Bousquets, J., E. González-Soriano & N. Papavero (eds.). Biodiversidad, taxonomía y biogeografía de artrópodos de México: hacia una síntesis de su conocimiento. Vol. II. CONABIO.

Kury, A.B., O. Villareal, M. & C. Sampaio. 2007. Redescription of the type species of *Cyuorta* (Arachnida, Opiliones, Cosmetidae). Journal of Arachnology 35:325–333.

Machado, G., P.C. Carrera, A.M. Pomini & A.J. Marsaioli. 2005. Chemical defense in harvestmen (Arachnida, Opiliones): Do benzoquinone secretions deter invertebrate and vertebrate predators? Journal of Chemical Ecology 31:2519–2539.

Mendes, A.C. 2011. Phylogeny and taxonomic revision of Heteropachylinae (Opiliones: Laniatores: Gonyleptidae). Zoological Journal of the Linnean Society 163:437–483.

Mendes, A.C. & A.B. Kury. 2007. Stygnopsidae Sorensen, 1932. Pp. 232–234. *In* Pinto-da-Rocha, R.G. Machado & G. Giribet (eds.). Harvestmen: The Biology of the Opiliones. Harvard University Press, Cambridge, Massachusetts.

Pérez-González, A. 2011. New familial assignment for two harvestmen species of the infraorder Grassatores (Arachnida: Opiliones: Laniatores). Zootaxa 2757:24–28.

Pinto-da-Rocha, R. & M.R. Hara. 2009. New familial assignment for three species of Neotropical harvestmen based on cladistic analysis (Arachnida: Opiliones: Laniatores). Zootaxa 2241:33–46.

Schwendinger, P.J. 2006. A taxonomic revision of the family Oncopodidae VI. *Martensiellus*, a new genus from Borneo, and the discovery of a tarsal pore organ in Oncopodidae (Opiliones: Laniatores). Zootaxa 1325:255–266.

Schwendinger, P.J. 2007. Oncopodidae Thorell, 1876. Pp. 211–214. *In* Pinto-da-Rocha, R., G. Machado & G. Giribet (eds.). Harvestmen: The Biology of the Opiliones. Harvard University Press, Cambridge, Masschusetts.

Schwendinger, P.J. & J. Martens. 2002. Penis morphology in Oncopodidae (Opiliones, Laniatores): evolutionary trees and relationships. Journal of Arachnology 30:425–434.

Sharma, P. & G. Giribet. 2009. Sandokanid phylogeny based on eight molecular markers—the evolution of a Southeast Asian endemic family of Laniatores (Arachnida, Opiliones). Molecular Phylogenetics and Evolution 52:432–447.

Sharma, P. & G. Giribet. 2011. The evolutionary and biogeographic history of the armoured harvestmen—Laniatores phylogeny based on ten molecular markers, with the description of two new families of Opiliones (Arachnida). Invertebrate Systematics 25:106–142.

Shear, W.A. 2006. *Marteusolasma jocheni*, a new genus and species of harvestman from Mexico (Opiliones: Nemastomatidae: Ortholasmatinae). Zootaxa 1325:191–198.

Shear, W.A. 2010. New species and records of ortholasmatine harvestmen from Mexico, Honduras, and the western United States (Opiliones, Nemastomatidae, Ortholasmatinae). ZooKeys 52:9–45.

Shultz, J.W. & R. Pinto-da-Rocha. 2007. Morphology and functional anatomy. Pp. 14–61. *In* Pinto-da-Rocha, R.G. Machado & G. Giribet (eds.). Harvestmen: The Biology of the Opiliones. Harvard University Press, Cambridge, Massachusetts.

Šilhavý, V. 1974. Cavernicolous opilionids from Mexico. Subterranean fauna of Mexico. Part. II. Quaderno Accademia Nazionale dei Lincei 170:175–194.

Šilhavý, V. 1977. Further cavernicolous opilionids from Mexico. Subterranean fauna of Mexico. Part III. Quaderno Accademia Nazionale dei Lincei 171:219–233.

Ubick, D. 2007. Phalangodidae Simon, 1879. Pp. 217–221. *In* Pinto-da-Rocha, R.G. Machado & G. Giribet (eds.). Harvestmen: The Biology the Opiliones. Harvard University Press, Cambridge, Massachusetts.

Vázquez, I.M. & J.C. Cokendolpher. 1997. *Guerrobuuus vallensis*, a new species of harvestman (Opiliones: Phalangodidae), from a cave in Valle de Bravo, state of Mexico, Mexico. Journal of Arachnology 25:257–261.

Villareal, M.O. & A.B. Kury. 2012. *Licornus* Roewer, 1932: newly transferred to Ampycinae and first record of the family Gonyleptidae (Opiliones: Laniatores) from Venezuela. Zootaxa 3544: 71–78.

Willemart, R.H., A. Pérez-González, J.P. Farine & P. Gnaspini. 2010. Sexually dimorphic tegumental gland openings in Laniatores (Arachnida, Opiliones), with new data on 23 species. Journal of Morphology 271:641–653.

Yamaguti, H.Y. & R. Pinto-da-Rocha. 2009. Taxonomic review of Bourguyiinae, cladistic analysis, and a new hypothesis of biogeographic relationships of the Brazilian Atlantic rainforest (Arachnida: Opiliones, Gonyleptidae). Zoological Journal of the Linnean Society 156:319–362.

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2013. The Journal of Arachnology 41:306–318

Notes on some species of the genus *Melanopa* (Opiliones: Sclerosomatidae: Gagrellinae) from China, with description of a new species

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Abstract. *Melanopa zhui,* a new species from Hunan Province, China, is described. *M. grandis* Roewer 1910 and *M. wangi* Zhu & Song 1999 are redescribed. The morphological characters and male genitalia of the three species are illustrated.

Keywords: Harvestmen, taxonomy, morphology, Palearctic region, Indo-Malaya region

Opilionids of the family Sclerosomatidae Simon 1879 are currently divided into subfamilies: Sclerosomatinae Simon 1879, Gagrellinae Thorell 1889, Leiobuninae Bank 1893 and Gyinae Šilhavý 1946, albeit unclearly delimited (Cokendolpher et al. 2007; Hedin et al. 2012). The genus *Melanopa* Thorell 1889 belongs to the subfamily Gagrellinae, and currently comprises 32 described species, which are mainly distributed throughout South Asia, Southeast Asia and East Asia (Roewer 1955; Suzuki 1982; Zhu & Song 1999; Kury 2012).

The genus *Melanopa* was erected by Thorell in 1889, based on the type species *M. plebeja* Thorell 1889 from Burma. With (1903) later synonymized this genus with *Gagrella* Stoliczka 1869, a decision that was rejected by Roewer in 1910 (Crawford 1992) due to the length of femora I and III being shorter than that of the body instead of longer than the body in *Gagrella*. Roewer (1955) reviewed *Melanopa*, and 33 species were recognized. He newly diagnosed the genus and provided three distinctive characters; e.g., a pseudoarticular nodule on femur II, a median spine on scute II, and the femora I and III shorter than the body.

Both *M. japonica* Roewer 1910 and *M. biseriata* Sato & Suzuki 1938 were synonymized with *Psathyropus tenuipes* L. Koch 1878 by Suzuki (1973). *Melanopa pumilio* Karsch 1881 was transferred to *Parammbogrella* Suzuki 1963 by Suzuki (1985). Suzuki (1982) and Zhu & Song (1999) each described a new species, *M. sumatrana* Suzuki 1982 and *M. wangi* Zhu & Song 1999. To date, no further detailed and thorough worldwide revisions were done except for aforementioned description and identification of species.

Previously, four *Melanopa* species have been recorded from China: *M. grandis* Roewer 1910, *M. similaris* Roewer 1955, *M. yunnanensis* Roewer 1910 and *M. wangi* Zhu & Song 1999. In this paper, *M. wangi* and *M. grandis* are redescribed and illustrated, based on the type specimens of *M. wangi* and new material of *M. grandis* collected from northeastern China. In addition, a new species is also recognized from Hunan Province, China, and is described under the name *M. zhui* new species.

METHODS

The specimens were preserved in 75% ethanol and were examined and drawn using a Leica M165c stereomicroscope equipped with a drawing tube. We studied further details using a compound Nikon YS100 microscope. The morphological terminology follows Hillyard & Sankey (1989). The terminology of genitalic structures follows Macías-Ordóñez et al. (2010) and Martens (1986). BLI follows Staręga (1972), which is abbreviated from "Beinlängenlindex" (index of leg length) and indicates the relation of the femur I length to the carapace width. Carapace width was measured between the incisions of coxae II and III, length from the anterior of carapace to the rear margin of the carapace medially. Opisthosoma width was measured at the widest point, length from anterior margin to the end medially. The cross-sectional shape of the shaft and glans refer to Martens (1978).

Specimens that we examined for this paper are deposited in the Museum of Hebei University, Baoding, China (MHBU). The following descriptions are based mostly on males; female characters, where notably different, are indicated. All measurements are given in mm. Abbreviations used in figures are as follows: Me = membrane; MS = microsetae; Mu = musculature; SD = sperm duct and Te = tendon.

TAXONOMY

Family Sclerosomatidae Simon 1879
Subfamily Gagrellinae Thorell 1889
Genus *Melanopa* Thorell 1889

Melanopa Thorell 1889:659; Roewer 1910:20; Roewer 1923:931; Roewer 1955:97; Crawford 1992:29.

Type species.—*Melanopa plebeja* Thorell 1889, by original designation.

Emended diagnosis (Palearctic species of *Melanopa* only).—Scute II with a median spine (scutes I and II each with a median spine in *M. ovata*: Sato & Suzuki 1938); only femur II with pseudoarticular nodule; male pedipalpal tibia with conspicuous ventral denticles. Penis lanceolate, shaft without sacs, the base of shaft with two large pieces of membrane; glans with an angle to the shaft in most species; glans without sensory seta; stylus short.

Composition.—33 species: *M. asperula* Roewer 1955, *M. atrata* (Stoliczka 1868), *M. cinctipes* Banks 1930, *M. dilata* Roewer 1929, *M. fragilis* (With 1903), *M. grandis* Roewer 1910, *M. guttata* Karsch 1881, *M. hansenii* (With 1903), *M. hirta* (With 1903), *M. impressata* Roewer 1955, *M. laciniipes* Roewer 1955, *M. maculipes* Banks 1930, *M. matherania* Roewer 1915, *M. nigra* Roewer 1955, *M. nigripes* Banks 1930, *M. ovata* Sato & Suzuki 1938, *M. peguana* Roewer 1955, *M. plebeja* Thorell 1889 (type species), *M. rugosa* Roewer 1955, *M. satoi* Roewer 1955, *M. scabra* Roewer 1912, *M. similaris* Roewer 1955, *M. sumatrana* Suzuki 1982, *M. thienemanni* Roewer 1931, *M. transversalis* Roewer 1912, *M. tristis* Thorell 1889, *M. trochanteralis* Roewer 1955, *M.*

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unicolor Roewer 1912, *M. varians* (With 1903), *M. vittata* Roewer 1910, *M. wangi* Zhu & Song 1999, *M. yuennanensis* Roewer 1910 and *M. zhui* new species.

Distribution.—China, Japan, Korea, Far East Russia, India, Sri Lanka, Sikkim, Nepal, Malaysia, Indonesia, Myanmar, and Vietnam.

Comments.—Male genitalia are not described for most known species of this genus, except *M. grandis* Roewer 1910, *M. satoi* Roewer 1955, *M. unicolor* Roewer 1912 and *M. wangi* Zhu & Song 1999. The male genitalia of these three species (*M. grandis*, *M. satoi*, *M. wangi*) have no alate part (sac), and these Palearctic species are distributed mainly in eastern Asia. In contrast, the male genitalia of *M. unicolor* have an alate part, and this species is found in southern Asia (see Diagnosis and Discussion).

Moreover, *M. guttata* Karsch 1881 and *M. ovata* Sato & Suzuki 1938 occur only in Japan. Although the males are unknown for either species, considering their distribution we tentatively place them amongst the Palearctic species. *Melanopa zhui* new species can no doubt also be referred to the Palearctic species-group based on its male genitalic morphology and distribution.

KEY TO PALEARCTIC SPECIES OF *MELANOPA*

1. Male (males of *M. guttata* and *M. ovata* are unknown) 2
   Female (female data of *M. satoi* not available) 5
2. Pedipalpal tibia ventrally with 3 enlarged denticles (Fig. 54; Roewer 1955: fig. 155; Suzuki 1986: fig. 42C) 3
   Pedipalpal tibia ventrally with 7 or more enlarged denticles (Figs. 9, 10, 31–32) 4
3. Proximal segment of chelicera with 3 dorsal teeth; shaft of penis with parallel sides (Figs. 51, 56) . . . *Melanopa zhui* new species
   Proximal segment of chelicera without dorsal teeth; shaft of penis with concave sides (Suzuki 1986: fig. 42B) . . . . *Melanopa satoi*
4. Shaft of penis with parallel sides, glans with tapered end (Figs. 15, 18, 19, 22) . . . . . *Melanopa grandis*
   Shaft of penis with concave sides, glans with truncated end (Figs. 33, 35, 36, 39) . . . . . *Melanopa wangi*
5. Scutes I and II each with a median spine (Sato & Suzuki 1938: fig. 3) . . . . . *Melanopa ovata*
   Scute II with a median spine 6
6. Pedipalpal femur as long as that of patella+tibia or tarsus (Sato & Suzuki 1938: 376) . . . . . *Melanopa guttata*
   Pedipalpal femur shorter than that of patella+tibia or tarsus (Table 1, 2, 3) 7
7. Proximal segment of chelicera with a ventral spur which has distal end blunt, without seta (Fig. 42) . . . . . *Melanopa wangi*
   Proximal segment of chelicera with a ventral setiferous spur (Fig. 65) 8
8. Pedipalpal tibia with many denticles ventrally and dorsally (Figs. 67, 68) . . . . . *Melanopa zhui* new species
   Pedipalpal tibia only with several denticles ventrally (Figs. 12, 13) . . . . . *Melanopa grandis*

Melanopa grandis Roewer 1910
Figs. 1–22

Melanopa grandis Roewer 1910:27; 1923:936–937; 1955:105; Suzuki 1960:25, fig. 7; 1965:355, fig. 1; 1972:65, fig. 1–3; 1973:8; 1986:31–32, fig. 40–41; Staręga 1978:208; Suzuki & Tsurusaki 1983:210; Tsurusaki 1982:12, fig. 5–7; 2006:153–154, fig. 6E–F; Tsurusaki & Sasaji 1991:18, fig. 8B; Li & Song 1993:241; Tchmeris 2000:41–45, fig. 42–53; Tsurusaki et al. 2005:52–55, fig. 2–5.

Metagagrella ussuriensis Redikorzew 1936:47–48, fig. 22–23; Roewer 1954:247; Staręga 1965:10–11; Gritsenko 1979a:33; 1979b:124–125, fig. 1–4. First synonymized with *M. grandis* by Tchmeris (2000).

Metagagrella damila Šilhavý 1976:297, fig. 1–12. First synonymized with *M. grandis* by Tsurusaki et al. (2005).

Gagrella crassitarsi Ha, Bae, Chun & Kim 2004:62, fig. 5–6. First synonymized with *M. grandis* by Tsurusaki et al. (2005).

Type specimens.—*M. grandis:* JAPAN: Holotype female, Tokyo (Zoologisches Institut und Museum, Hamburg), not examined.

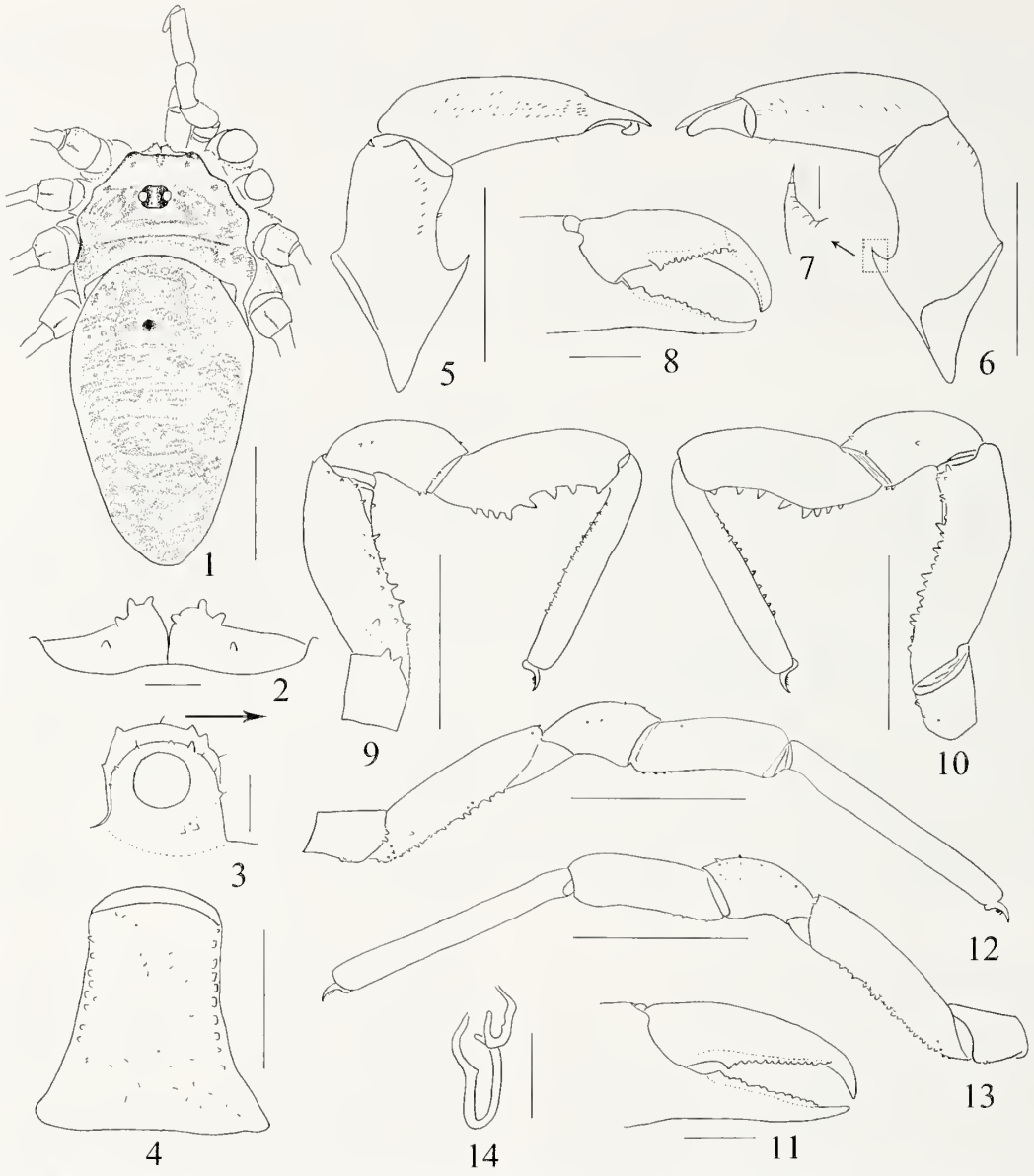
Material examined.—CHINA: *Jilin Province*: 3 ♂, 4 ♀, Huadian City, Jiapigou Town, 580 m, 42°53′N, 127°34′E, 7 August 2011, C. Zhang (MHBU); 1 ♂, 2 ♀, Antu County, Erdaobaihe Town, 865 m, 42°19′N, 128°07′E, 12 August 2011, B.S. Zhang and H.M. Yu (MHBU); *Liaoning Province*: 3 ♂, 6 ♀, Xinbin County, Nanzamu Town, 210 m, 41°56′N, 124°24′E, 22 August 2011, C. Zhang (MHBU).

Diagnosis.—*Melanopa grandis* can be recognized by the following characters: 1) male pedipalpal tibia ventrally with 7–8 enlarged denticles; 2) shaft of penis with nearly parallel sides, flattened dorsally and arched ventrally; 3) glans arched dorsally and ventrally.

Redescription.—*Coloration:* Dorsum with brown background. Preocular region of propeltidium with a large white fleck, each side of ocular region with rusty brown flecks covered with a few whitish dots, post-optic region with a triangular dark brown fleck. Ocularium brown, with blackish eye rings and a pale dorsal band. Meso- and metapeltidium rusty brown. Metapeltidium with imperfect transverse rows of white spots medially and darker patches laterally. Opisthosomal scute with obscure dark brown saddle, darker anteriorly and posteriorly, lighter between. Many white spots on the saddle surface. Lateral saddle and free tergites brown to dark brown and with numerous white spots.

Venter: Coxae I–IV brown. Genital operculum rusty yellow. Sternites rusty yellow to dark brown at middle, with light brown patches laterally. Chelicerae yellow. Pedipalpus yellowish brown, femur and patella blackish brown, tarsus yellow. Legs yellowish brown to dark brown, patella blackish brown and apical tibiae pale yellow.

Dorsum (Fig. 1)*:* Entire body leathery, dorsum covered with rather fine granules. Carapace without any denticles. Supracheliceral laminae with four tubercles on each lamina (Fig. 2). Ozopores small and visible from above. Ocularium average-sized (about 1/6 of width and 2/7 of length of carapace) with a



Figures 1–14.—*Melanopa grandis* Roewer 1910, from Jiapigou Town (42°53′N, 127°34′E): 1–10: male; 11–14: female. 1. Dorsal aspect of body; 2. Dorsal aspect of supracheliceral laminae; 3. Lateral aspect of ocularium; 4. Ventral aspect of genital operculum; 5. Medial aspect of left chelicera; 6. Ectal aspect of left chelicera; 7. Ectal aspect of left ventral setiferous spur; 8. Frontal aspect of left fingers; 9. Medial aspect of left pedipalpus; 10. Ectal aspect of left pedipalpus; 11. Medial aspect of left pedipalpus; 12. Ectal aspect of left pedipalpus; 13. Frontal aspect of left fingers; 14. Seminal receptacle. Scale = 2 mm (1); 1 mm (4–6, 9–10, 12–13); 0.2 mm (2, 3, 8, 11); 0.1 mm (7); 0.05 mm (14).

medial groove and rows of tubercles on the carinae and two tubercles beneath each eye (Fig. 3). Scute II with a strong spine, remaining opisthosomal tergites smooth.

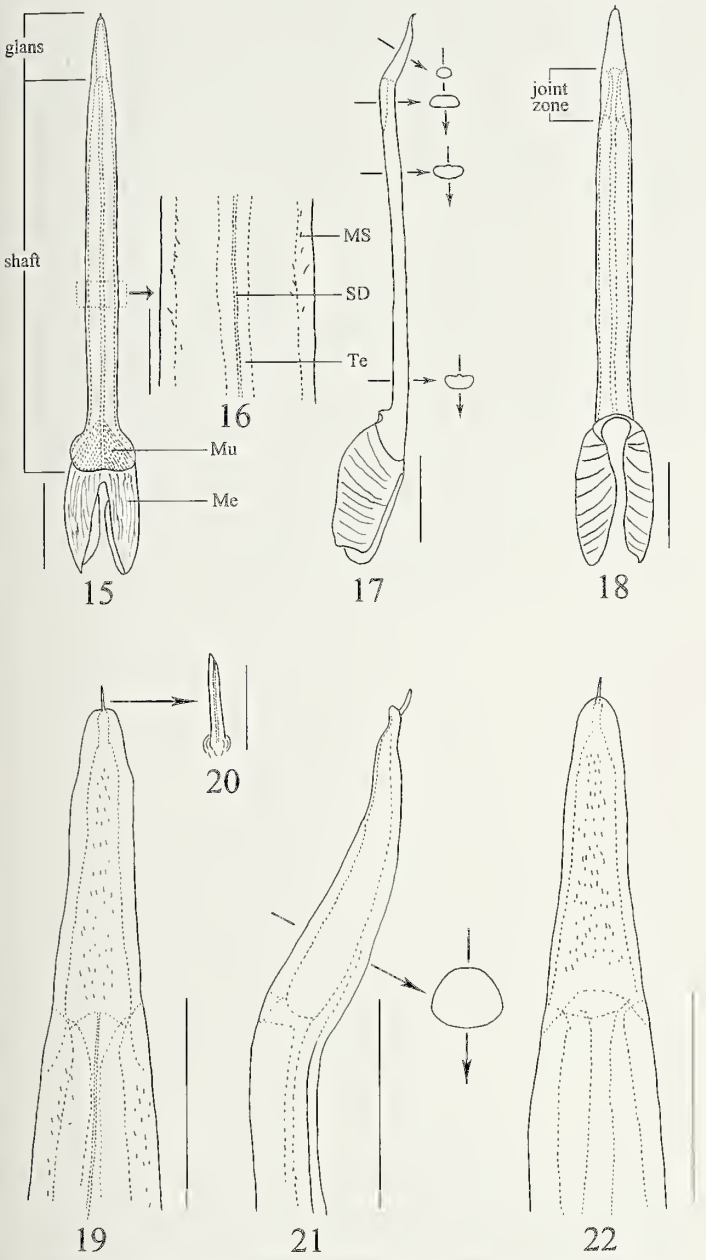
Venter: Surface of all coxae roughly granular, all coxae anteriorly and coxae I and IV posteriorly with a row of subquadratic marginal tubercles, lateral row of similar tubercles on each side of genital operculum. Genital operculum (Fig. 4) almost trapezioid, surface with sparse setae. Opisthosomal sternites smooth, with sparse setae.

Chelicera (Figs. 5–8)*:* Proximal segment with a ventral setiferous spur (Fig. 7), with only a few dorsal setae and two ventral setae, also and a row of medial setae. Second segment with setae on the frontal surface, and numerous short medial setae. Inner edges of fingers toothed as illustrated (Fig. 8): teeth on the fingers serrated, the basal tooth is the largest.

Pedipalpus (Figs. 9, 10)*:* Trochanter with two conspicuous distomesal and ventral denticles. Femur ventrally with numerous dense denticles, on the medial basal side with one denticle, on the same distal margin having a few denticles. Patella with two medial and one ectal denticles, distal margin with a few denticles. Tibia swollen at base, ventrally with a row of eight enlarged denticles. Tarsus ventrally with two longitudinal rows of microdenticles, medial dentition longer than ectal one. Remainder of each pedipalpal segment only with hair. Claw with teeth.

Legs: All trochanters prolaterally and retrolaterally with many denticles. Femur, patella and tibia with rows of teeth, the rest of each segment only with rows of setae. Nodule formula 0/1/0/0.

Penis (Figs. 15–22)*:* Shaft with nearly parallel sides, abruptly widened basally, gradually narrower in joint zone



Figures 15–22.—*Melanopa grandis* Roewer 1910, male from Jiapigou Town (42°53′N, 127°34′E). 15. Ventral aspect of penis; 16. Ventral aspect of shaft (part); 17. Lateral aspect of penis; 18. Dorsal aspect of penis; 19. Ventral aspect of glans; 20. Ventral aspect of stylus; 21. Lateral aspect of glans; 22. Dorsal aspect of glans. Scale = 1 mm (15, 17–18); 0.5 mm (19, 21–22); 0.2 mm (16); 0.05 mm (20).

and extending to a finger-shaped glans. Shaft flattened dorsally and arched ventrally, medial shaft dorsally bulgy and ventral surface with sparse microsetae along both sides of the shaft. In contrast, joint zone flattened ventrally and dorsal surface tapered into the glans, both sides of joint zone with more microsetae than ventral surface. Sperm duct conspicuously visible in the joint zone. Musculature limited to basal shaft and membranes. Glans slightly bent, holding at about 160° with shaft. Glans widest at base, gradually narrower toward blunt end. Dorsal surface arched strongly and ventral slightly, both central surface with many microsetae. Stylus short, cylindrical, inserted ventrally near apex of glans and with a bevel apex.

Female (Figs.11–14)*:* Similar to male but much larger, and abdomen wide. Cheliceral fingers longer than the male, inner edges toothed as illustrated (Fig. 11). Pedipalpal tibia normal, ventrally with reduced denticles at base, tarsus without any denticles and micro-denticles (Figs. 12, 13).

Seminal receptacle (Fig. 14)*:* Between segments two and three, consisting of a small anterior and a large posterior ampulla.

Measurements: Male (female): body 7.10 (7.90) long. Carapace 1.90 (2.15) long, 3.00 (2.80) wide. Opisthosoma 5.20 (5.75) long, 3.15 (3.90) wide. BLI 2.08 (2.05). Eye tubercle 0.42 (0.40) long, 0.56 (0.53) wide, 0.40 (0.40) high. Penis shaft 4.45 long, 0.75 wide at base, glans 0.41 long, stylus 0.06 long. Measurements of left pedipalpus and right legs as in Table 1.

Variation.—Size range of male (female). Body length 7.00–7.50 (7.90–9.00). Carapace length 1.85–2.13 (2.15–2.25), width 3.15–3.63 (2.80–3.55); opisthosoma length 5.25–5.38 (5.75–6.63), width 3.00–3.33 (3.90–4.38).

Habitat.—The specimens were collected with an entomological net or picked from low foliage and tree trunks in the forest.

Distribution.—China, Russia, Japan and Korea.

Melanopa wangi Zhu & Song 1999
(Figs. 23–46)

Melanopa wangi Zhu & Song 1999:160, 162, fig. 2.

Type material.—CHINA: *Hunan Province:* Holotype male, Zhangjiajie National Forest Park (29°08′N, 111°25′E), Zhangjiajie City, 20 August 1990, M.S. Zhu (MHBU), examined. Paratypes: 1 ♂, 1 ♀, collected with holotype (MHBU), examined.

Diagnosis.—This species is recognized by the following characters: 1) male pedipalpal tibia ventrally with many denticles; 2) shaft of penis with concave sides, flattened ventrally, and arched dorsally; and 3) glans with truncated end, flattened ventrally and arched dorsally.

Redescription.—*Coloration:* dorsum with rusty brown background. Propeltidium with many dark brown markings around ocular region. Ocularium rusty brown, with blackish eye rings and a pale dorsal band. Meso- and metapeltidium each with a transverse row of blackish brown streak. Saddle on opisthosomal scute imperfect, only median part of scutes I and II blackish-brown. Remainder scutes and free tergites with blackish brown dots and cross stripes.

Venter: Coxae I–IV, genital operculum and sternites rusty brown, sternites with many black flecks. Proximal segment of chelicerae rusty yellow, second segment rusty brown and with some black flecks frontally. Pedipalpus yellowish brown, femur and patella blackish brown, tibia and tarsus with many blackish flecks. Legs rusty brown, trochanter, and femur blackish brown.

Dorsum (Fig. 23)*:* Entire body leathery, dorsum covered with rather fine granules. Carapace without any denticles. Supracheliceral laminae with many tubercles on each lamina (Fig. 24). Ozopores small and visible from above. Ocularium average-sized (about 1/6 of width and 1/4 length of carapace), rounded dorsally, canaliculate, almost smooth, only with sparse hairs (Fig. 25). Scute II with a strong spine, remaining opisthosomal tergites smooth.

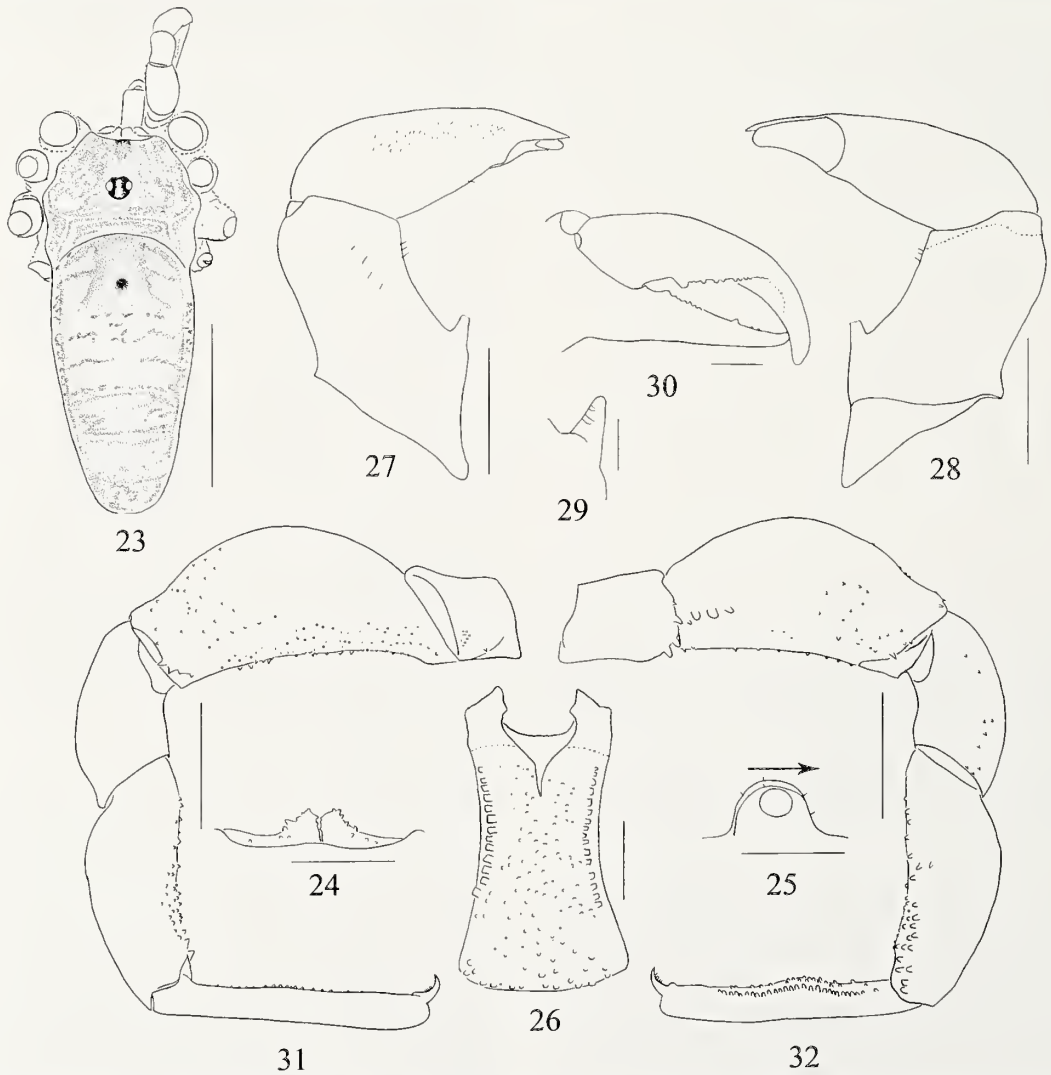
Table 1.—Pedipalpus and legs measurements of the male (female) of *Melanopa grandis*.

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
Pedipalpus	0.50(0.40)	1.15(1.00)	0.84(0.70)	0.95(0.73)		1.35(1.46)	4.79(4.29)
Leg I	0.60(0.65)	6.25(5.75)	1.50(1.50)	5.90(5.00)	7.50(6.75)	11.25(9.50)	33.00(29.15)
Leg II	0.60(0.65)	11.50(10.75)	1.50(1.50)	11.25(10.50)	11.90(10.75)	21.00(21.50)	57.75(55.65)
Leg III	0.60(0.65)	6.25(5.75)	1.50(1.50)	5.50(4.75)	8.00(7.25)	11.00(9.25)	32.85(29.15)
Leg IV	0.60(0.65)	9.25(6.40)	1.50(1.50)	7.65(5.25)	11.50(8.10)	14.90(9.10)	45.40(31.00)

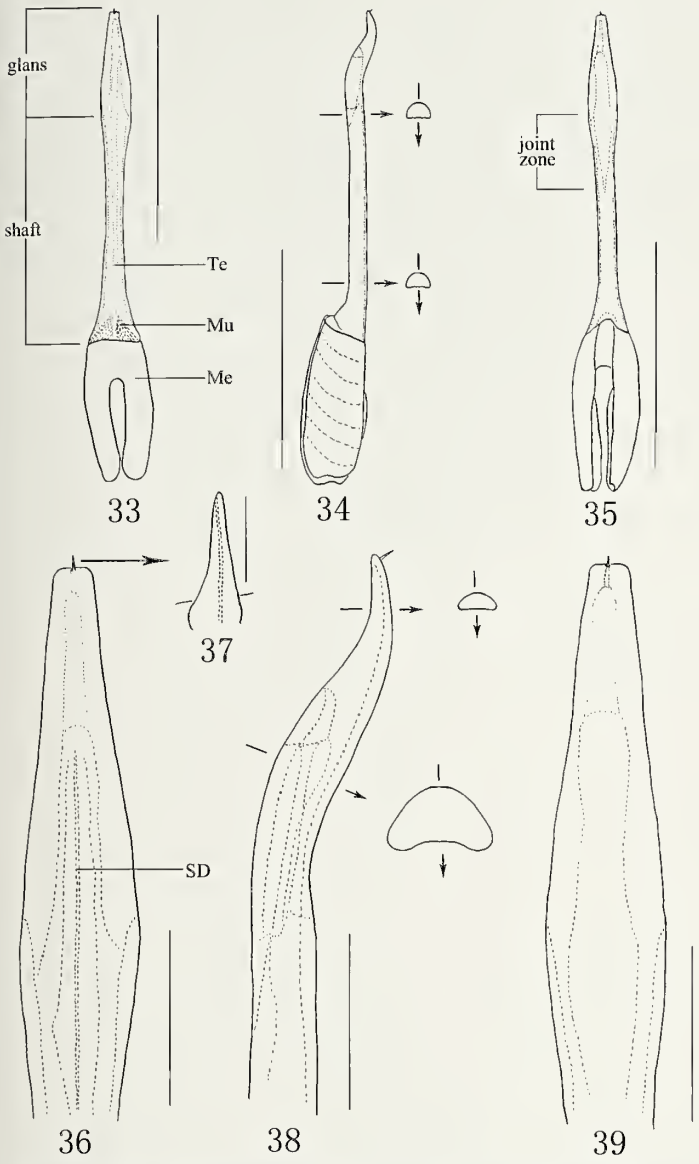
Venter: Surface of all coxae roughly granular, all coxae anteriorly and coxae I and IV posteriorly with a row of subquadratic marginal tubercles, a lateral row of similar tubercles on each side of genital operculum. Genital operculum (Fig. 26) surface with many granules, anterior margin with a wide median cleft, lateral margin somewhat concave, almost twice as long as posterior margin. Opisthosomal sternites smooth, with sparse setae.

Chelicera (Figs. 27–29)*:* Proximal segment with a ventral spur (Fig. 29), distal end blunt, without seta, with only a few dorsal and ventral setae, and a row of medial setae. Second segment with setae on the frontal surface and numerous short medial setae. Inner edges of fingers toothed as illustrated (Fig. 30): discontinuous teeth on the fingers serrated, fixed finger more conspicuous than moveable finger, the basal tooth largest.

Pedipalpus (Figs. 31, 32)*:* Trochanter with four conspicuous distomesal and a few ventral denticles, femur strongly swollen in medial part, with numerous dense denticles except distodorsal side, with four conspicuous denticles on medial basal



Figures 23–32.—*Melanopa wangi* Zhu & Song 1999, male (holotype) from Zhangjiajie City (29°08′N, 111°25′E). 23. Dorsal aspect of body; 24. Dorsal aspect of supracheliceral laminae; 25. Lateral aspect of ocularium; 26. Ventral aspect of genital operculum; 27. Medial aspect of left chelicera; 28. Ectal aspect of left chelicera; 29. Ectal aspect of right ventral spur; 30. Frontal aspect of left fingers; 31. Ectal aspect of left pedipalpus; 32. Medial aspect of left pedipalpus. Scale = 5 mm (23); 1 mm (24–28, 31–32); 0.2 mm (29–30).



Figures 33–39.—*Melanopa wangi* Zhu & Song 1999, male (holotype) from Zhangjiajie City (29°08′N, 111°25′E). 33. Ventral aspect of penis; 34. Lateral aspect of penis; 35. Dorsal aspect of penis; 36. Ventral aspect of glans; 37. Ventral aspect of stylus; 38. Lateral aspect of glans; 39. Dorsal aspect of glans. Scale = 5 mm (33–35); 1 mm (36, 38–39); 0.05 mm (37).

side. Patella with a few medial denticles. Tibia swollen at base, ventrally with many conspicuous denticles. Tarsus somewhat swollen ventrally in middle part, ventrally with a longitudinal row of micro-denticles as well as many scattered similar denticles. Remainder of each pedipalpal segment only with hair. Claw with teeth.

Legs: All trochanters prolaterally and retrolaterally with many denticles. Femur, patella and tibia with rows of teeth, rest of each segment only with rows of setae. Nodule formula 0/4/0/0.

Penis (Figs. 33–39)*:* Sides of shaft concave, widened distally and proximally. Shaft flattened ventrally and arched dorsally. Both sides of joint zone and basal glans with many microsetae. Sperm duct conspicuously visible in the joint zone. Musculature limited to basal shaft and membranes. Glans slightly bent, holding at about 160° with shaft, reflexed distally. Glans widest at base, gradually narrower toward truncated end, dorsal surface arched and ventral flattened. Stylus short, conical from ventral view, inserted ventrally near apex of glans.

Female (Figs. 40–46)*:* Similar to male but body slightly shorter and wider. Anterior margin of genital operculum (Fig. 41) with a wide median cleft. Inner edges of cheliceral fingers toothed as illustrated (Fig. 43), both fixed finger and moveable finger with continuous teeth. Pedipalpus normal, tarsus without any denticles (Figs. 44, 45).

Seminal receptacle (Fig. 46)*:* Between segments two and three, consisting of a small and a large ampullae.

Measurements: Male (female): body 11.75 (7.90) long. Carapaee 3.00 (2.90) long, 4.75 (4.55) wide. Opisthosoma 8.75 (5.90) long, 3.90 (5.25) wide. BLI 2.11 (2.03). Eye tubercle 0.70 (0.60) long, 0.78 (0.70) wide, 0.55 (0.50) high. Penis 7.50 long: shaft 5.25 long, 1.16 wide at base; glans 2.25 long, 0.65 wide at base; stylus 0.09 long. Measurements of left pedipalpus and right legs as in Table 2.

Habitat.—Unknown.

Distribution.—China.

Melanopa zhui new species
(Figs. 47–69)

Type material.—CHINA: *Hunan Province*, Holotype male, Zhangjiajie City, Zhangjiajie National Forest Park, 29°08′N, 111°25′E, 20 August 1990, M.S. Zhu (MHBU). Paratype: 1 ♀, collected with holotype (MHBU).

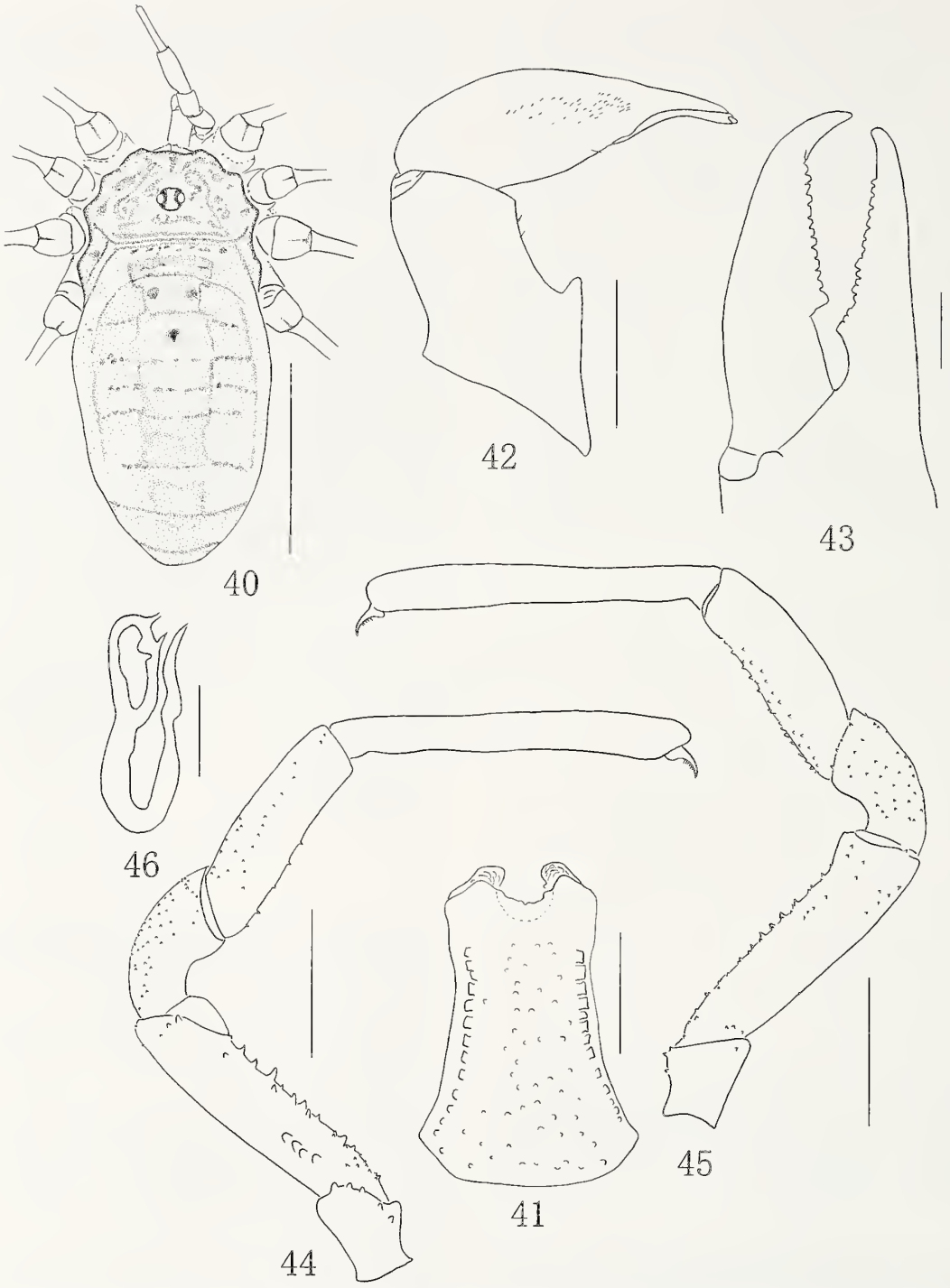
Etymology.—The specific name is a patronym in honor of the late Professor Mingsheng Zhu (1950–2010), a well known arachnologist in China.

Diagnosis.—Recognized by the following characters: 1) male pedipalpal tibia distally with three ventral denticles; 2) Shaft flattened ventrally, both sides of dorsal surface bulgy in form of the shallow U-shaped cross section and 3) glans not bent, base dorsally with median pit.

Description.—*Coloration:* dorsum with rusty yellow background. Propeltidium with many brown markings around ocular region. Ocularium yellow, with blackish eye rings and a pale dorsal band. Meso- and metapeltidium rusty brown with two lateral yellow flecks. Saddle on opisthosomal scute inconspicuous, only median part of scutes I–II and V blackish

Table 2.—Pedipalpus and legs measurements of the male (female) of *Melanopa wangi.*

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
Pedipalpus	0.85(0.55)	2.20(1.60)	1.50(1.08)	1.65(1.36)		2.10(2.60)	8.30(7.19)
Leg I	1.25(1.00)	10.00(9.25)	2.50(2.25)	9.00(8.00)	12.75(11.50)	14.00(14.50)	49.50(46.50)
Leg II	1.25(1.00)	21.00(17.25)	2.50(2.25)	21.00(17.50)	21.75(19.50)	42.50(40.00)	110.00(97.50)
Leg III	1.25(1.00)	9.25(8.50)	2.50(2.25)	9.25(7.25)	12.75(10.75)	15.50(14.00)	50.50(43.75)
Leg IV	1.25(1.00)	13.75(12.25)	2.50(2.25)	12.00(10.25)	19.75(16.25)	20.25(19.75)	69.50(62.00)

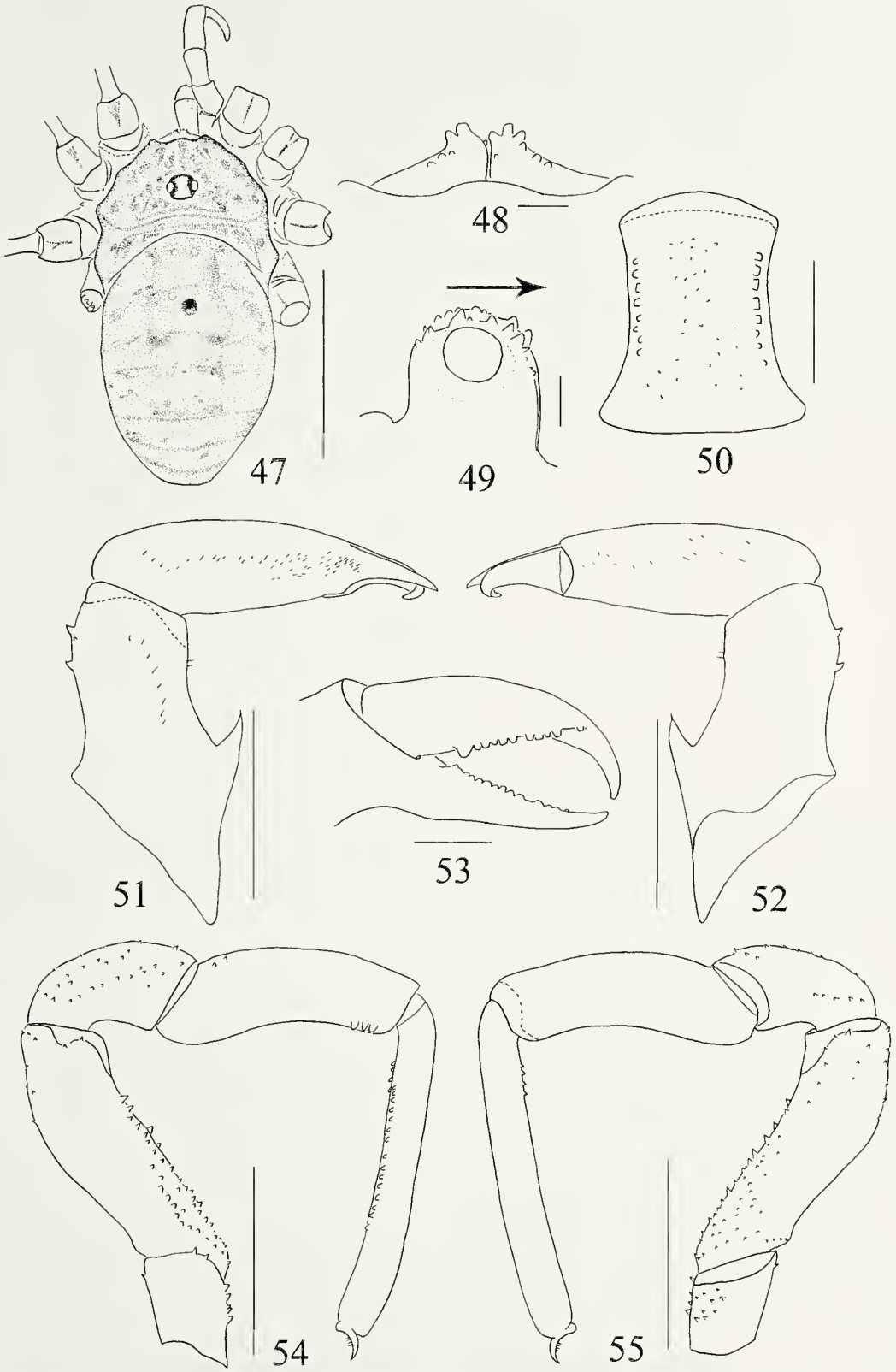


Figures 40–46.—*Melanopa wangi* Zhu & Song 1999, female (paratype) from Zhangjiajie City (29°08′N, 111°25′E). 40. Dorsal aspect of body; 41. Ventral aspect of genital operculum; 42. Medial aspect of left chelicera; 43. Frontal aspect of left fingers; 44. Ectal aspect of left pedipalpus; 45. Medial aspect of left pedipalpus; 46. Seminal receptacle. Scale = 5 mm (40); 1 mm (41–42, 44–45); 0.2 mm (43); 0.05 mm (46).

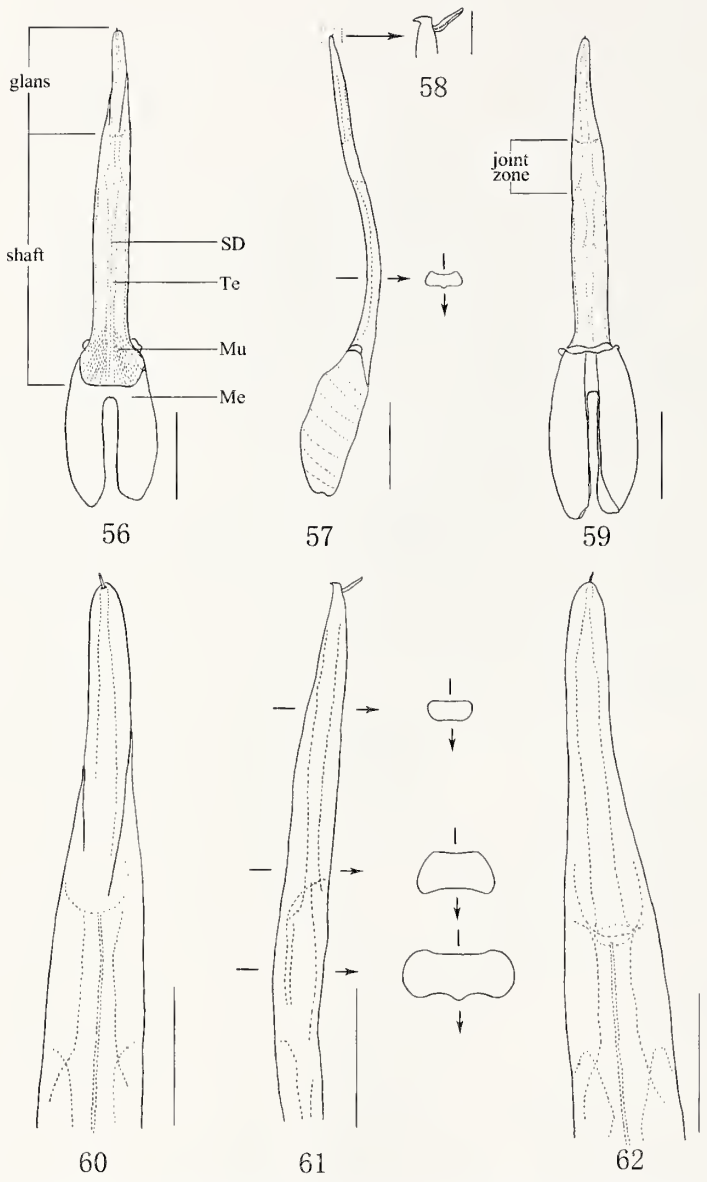
brown. Remainder scutes and free tergites with dark brown dots and cross stripes.

Venter: Coxae I–IV and genital operculum dark rusty brown, sternites rusty yellow and with many dark brown flecks in median section. Chelicerae yellow, proximal segment with dark brown patches dorsally and ventrally, second segment with the same color stripes medially and ectally. Pedipalpus: trochanter, femur, patella and basal tibia brown, remaining part of tibia and tarsus yellow. Legs rusty brown, trochanter yellow dorsally and dark brown ventrally, metatarsus and tarsus somewhat lighter.

Dorsum (Fig. 47)*:* Entire body leathery, dorsum covered with rather fine granules. Carapace without any denticles. Supracheliceral laminae with a few tubercles on each lamina (Fig. 48). Ozopores small and visible from above. Ocularium average-sized (about 1/6 of width and 1/3 of length of



Figures 47–55.—*Melanopa zhui* new species, male (holotype) from Zhangjiajie City (29°08′N, 111°25′E). 47. Dorsal aspect of body; 48. Dorsal aspect of suprachelicerai laminae; 49. Lateral aspect of ocularium; 50. Ventral aspect of genital operculum; 51. Medial aspect of left chelicera; 52. Ectal aspect of left chelicera; 53. Frontal aspeet of left fingers; 54. Ectal aspect of left pedipalpus; 55. Medial aspect of left pedipalpus. Scale = 5 mm (47); 1 mm (50–52, 54–55); 0.2 mm (48–49, 53).



Figures 56–62.—*Melanopa zhui* new species, male (holotype) from Zhangjiajie City (29°08′N, 111°25′E). 56. Ventral aspect of penis; 57. Lateral aspect of penis; 58. Lateral aspect of distal glans; 59. Dorsal aspect of penis; 60. Ventral aspect of glans; 61. Lateral aspect of glans; 62. Dorsal aspect of glans. Scale = 1 mm (56–57, 59); 0.5 mm (60–62); 0.1 mm (58).

carapace), rounded dorsally, canaliculate, with a few tubercles on the carinae (Fig. 49). Scute II with a strong spine, remaining opisthosomal tergites smooth.

Venter: Surface of all coxae roughly granular, all coxae anteriorly and coxae I and IV posteriorly with a row of subquadratic marginal tubercles, a lateral row of similar tubercles on each side of genital operculum. Genital operculum (Fig. 50) surface with sparse granules, anterior margin convex, lateral margin slightly concave, almost with the same length as posterior margin. Opisthosomal sternites smooth, with sparse setae.

Chelicera (Figs. 51–53)*:* Proximal segment with a ventral setiferous spur and three dorsal teeth. Second segment with setae on the frontal surface, and numerous short medial setae. Inner edges of fingers toothed as illustrated (Fig. 53): discontinuous teeth on the fingers serrated, the basal tooth largest.

Pedipalpus (Figs. 54, 55)*:* Trochanter with two conspicuous distomesal and many ventral denticles. Femur ventrally with numerous dense denticles. Patella with many denticles except for ventral side. Tibia slightly swollen at base, dorsally with two basal denticles, distally with three ventral denticles. Tarsus ventrally with a longitudinal row of micro-denticles just lateral of these denticles, with another row of four micro-denticles basally. Remainder of each pedipalpal segment only with hair. Claw with teeth.

Legs: All trochanters prolaterally and retrolaterally with many denticles. Femur, patella, and tibia with rows of teeth, the rest of each segment only with rows of setae. Nodule formula 0/2/0/0.

Penis (Figs. 56–62)*:* Shaft short, with nearly parallel sides, basal part abruptly widened. Shaft flattened ventrally, both sides of dorsal surface bulgy in form of the shallow U-shaped cross section. Joint zone flattened dorsally and ventrally, ventral surface medially bulgy. Sperm duct conspicuously visible in the joint zone. Musculature limited to basal shaft and membranes. Glans not bent, base dorsally with median pit. Dorsal surface of glans widest at base, ventral base as long as the end of glans, flattened dorsally and ventrally. End of glans with a dorsal projection, some rather beak-like from lateral view. Stylus short, cylindrical, inserted ventrally near apex of glans and with a bent base from lateral view.

Female (Figs. 63–69)*:* Similar to male and about the same size. Anterior margin of genital operculum (Fig. 64) with a wide median cleft. Inner edges of cheliceral fingers toothed as illustrated (Fig. 66), both fixed finger and moveable finger with continuous teeth. Pedipalpus normal, tibia with many denticles dorsally and ventrally, tarsus without any denticles (Figs. 67, 68).

Seminal receptacle (Fig. 69)*:* Between segments two and three, consisting of a small anterior and a large posterior ampullae.

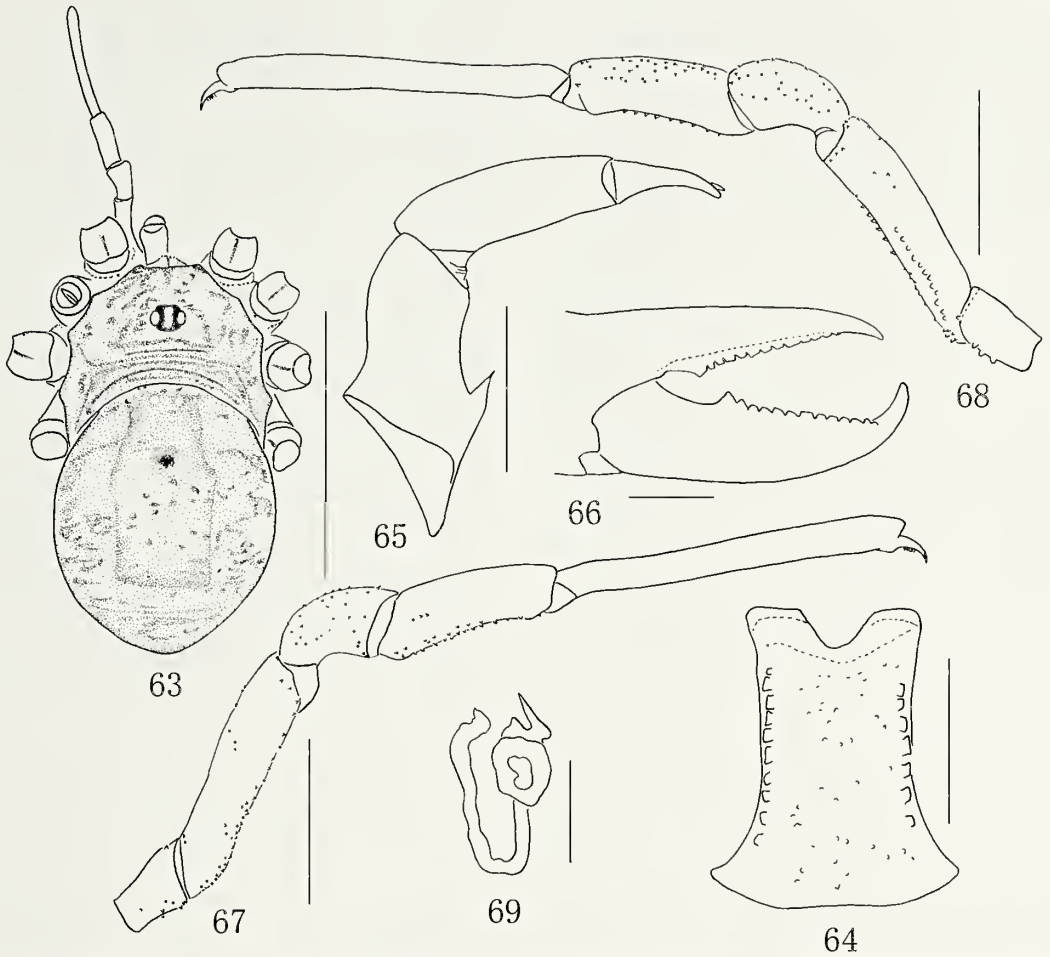
Measurements: Male (female): body 7.13 (7.50) long. Carapace 1.88 (2.00) long, 3.70 (3.63) wide. Opisthosoma 5.25 (5.50) long, 3.58 (4.25) wide. BLI 2.23 (2.18). Eye tubercle 0.48 (0.50) long, 0.68 (0.65) wide, 0.55 (0.50) high. Penis 4.18 long, shaft 3.00 long, 0.93 wide at base; glans 1.18 long; stylus 0.09 long. Measurements of left pedipalpus and right legs as in Table 3.

Habitat.—Unknown.

Distribution.—China.

DISCUSSION

Roewer's typological classification of Gagrellinae has been rather chaotic (Crawford 1992; Tourinho & Kury 2001; Klimeš 2006; Cokendolpher et al. 2007; Taylor 2009; Hedin et al. 2012) and almost the whole classification system of Roewer is artificial (Tourinho 2007; Giribet et al. 2012; Hedin et al. 2012). Roewer (1910, 1923, 1955) defined *Melanopa* by external characters such as only femur II with one pseudoarticular nodule, scute II with one median spine or scutes I–II each with one median spine, ocularium with or without tubercles, and femora I and III shorter than the body. However, he ignored the male genitalia (penis), which can be very important for harvestman classification, and his system is



Figures 63–69.—*Melanopa zhui* new species, female (paratype) from Zhangjiajie City (29°08′N, 111°25′E). 63. Dorsal aspect of body; 64. Ventral aspect of genital operculum; 65. Ectal aspect of right chelicera; 66. Frontal aspect of right fingers; 67. Ectal aspect of right pedipalpus; 68. Medial aspect of right pedipalpus; 69. Seminal receptacle. Scale = 5 mm (63); 1 mm (64–65, 67–68); 0.2 mm (66); 0.05 mm (69).

unlikely to be phylogenetically accurate (Tourinho & Kury 2001; Hedin et al. 2012).

The external characters mentioned above are often highly variable. Foremost among the characters to delimit the genus has been the number of pseudoarticular nodules in the femora of the legs (Taylor 2009); however, the number of nodules is inconsistent (Suzuki 1973; Martens 1987; Tourinho-Davis 2004; Klimeš 2006), and is not suitable to define *Melanopa*. Other variable characters used to define *Melanopa* are the relative length of the legs with respect to the body, the armature of the scutae or the ocularium. It is evident that when the genus *Melanopa* is based on these characters it tends to conceal natural phylogenetie patterns. Comparing the penis of *M. unicolor* Roewer 1912 with that of *M. grandis* Roewer 1910 and *M. satoi* Roewer 1955 (the penis of *M. unicolor* with alate part, while that of *M. grandis* and *M. satoi* without alate part, cf. Suzuki 1966:115–116, fig. 1; 1986:31–33, fig. 40, 42) demonstrates the disparity in this genus.

In addition, by not considering penis morphology, Roewer also failed to take biogeography into account. Recent research has shown that "geography is better than taxonomy in predicting phylogeny" in sclerosomatid harvestmen based on molecular data (Hedin et al. 2012). The limited dispersal ability of Opiliones makes many harvestmen groups prime candidates for biogeographic studies (e.g., Giribet & Kury 2007:77–78).

Although we have not examined most species of *Melanopa*, including the type species, and we have not carried out a full systematic revision combining external and genitalic characters, we are able to make some preliminary observations regarding this genus. On the basis of biogeography, we tentatively suggest dividing the genus into two groups: one including five species occurring in the Palearctic region, the other including 27 species recorded from the Indo-Malaya region (Table 4).

The five previously described species in the Palearctic region are *M. grandis*, *M. guttata* Karsch 1881, *M. ovata* Sato & Suzuki 1938, *M. satoi,* and *M. wangi* Zhu & Song 1999. *Melanopa guttata*, *M. ovata,* and *M. satoi* are distributed in Japan, and *M. wangi* is so far known only from Hunan Province, China. *Melanopa grandis* is widely distributed throughout Japan, the Korean peninsula and northern China. Additionally, two other species found in Yunnan Province, southern China, *M. yuennanensis* Roewer 1910 and *M. similaris* Roewer 1955, are included in the Indo-Malayan group.

The five Palearctic species show great similarity to each other in external morphology; e.g., scute II with a median

Table 3.—Pedipalpus and legs measurements of the male (female) of *Melanopa zhui*.

	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
Pedipalpus	0.45(0.50)	1.33(1.25)	0.90(0.75)	1.10(0.95)		1.80(2.00)	5.58(5.45)
Leg I	0.75(0.75)	8.25(7.90)	2.00(1.75)	6.40(6.00)	7.90(7.90)	11.50(12.50)	36.80(36.80)
Leg II	0.75(0.75)	15.25(14.00)	2.00(1.75)	14.50(13.25)	12.60(13.75)	28.00(25.50)	73.10(69.00)
Leg III	0.75(0.75)	8.10(7.75)	2.00(1.75)	6.25(5.75)	8.25(8.25)	6.75(11.25)	32.10(35.50)
Leg IV	0.75(0.75)	11.50(11.25)	2.00(1.75)	8.50(7.75)	12.50(12.50)	14.50(14.75)	49.75(48.75)

spine (scutes I and II each with a median spine in *M. ovata*); femur II with a single pseudoarticular nodule; and pedipalpal tibia with conspicuous ventral denticles in the male. With the exception of *M. guttata* and *M. ovata* (known only from female specimens), the remaining three species (*M. grandis*, *M. satoi* and *M. wangi*) possess similar penes; e.g., penis simple: shaft without a dorsal sheath, ventral lamella, pocket, sacs or ventro-basal opening, base of shaft with two large pieces of membrane; joint zone of shaft and glans inconspicuous; glans without sensory seta; and the stylus short.

Although *M. zhui* is placed with the Palearctic species, there are still some differences between them. *Melanopa zhui* can be distinguished from *M. ovata* by scute I without a median spine, the pedipalpal patella and tibia with more denticles, ocularium with more tubercles (Sato & Suzuki 1938:376–379, fig. 4); the description of *M. guttata* provided by Roewer (1923, 1955) was brief and the figure very schematic, and it only can be distinguished from *M. zhui* by the color of body (Roewer 1923:938; Roewer 1955:105, fig. 154).

Comparing *Melanopa zhui* with the other three species with known males, the new species can be distinguished by having three ventral denticles distally on the pedipalpal tibia of the male, compared to a row of 7–8 ventral denticles in *M. grandis*, many ventral denticles in *M. wangi* and three almost evenly distributed ventral denticles in *M. satoi* (Roewer 1955:105, fig. 155; Suzuki 1986:33, fig. 42C). The most

Table 4.—Geographical distribution of the species of *Melanopa*.

No.		Species	Distribution	References
Palearctic region	1	*M. grandis* Roewer 1910	China, Japan, Korea and Far East Russia	Tsurusaki et al. (2005)
	2	*M. guttata* Karsch 1881	Japan	Roewer (1955)
	3	*M. ovata* Sato & Suzuki 1938	Japan (Nagano-ken)	Sato & Suzuki (1938)
	4	*M. satoi* Roewer 1955	Japan (bei Jokohama)	Roewer (1955); Suzuki (1986)
	5	*M. wangi* Zhu & Song 1999	China (Hunan Province)	Zhu & Song (1999)
	6	*M. zhui* new species	China (Hunan Province)	this paper
Indo-Malaya region	1	*M. matherania* Roewer 1915	Dekan (Matheran)	Roewer (1955)
	2	*M. rugosa* Roewer 1955	Dekan (Ootokamund)	Roewer (1955)
	3	*M. trochanteralis* Roewer 1955	Nilgiris	Roewer (1955)
	4	*M. fragilis* (With 1903)	Sikkim, Darjiling, Burma, Pashok, Himalaya, Kurseong, Pashok, Dawna Hills, Ghumti	Roewer (1955)
	5	*M. atrata* (Stoliczka 1868)	Bengalen, Himalaya, Calcutta, Bengalen	Roewer (1955)
	6	*M. varians* (With 1903)	Bengalen, Burma	Roewer (1955)
	7	*M. hansenii* (With 1903)	Vorderindien (Todaspoor)	Roewer (1955)
	8	*M. hirta* (With 1903)	Punkabari, Darjiling	Roewer (1955)
	9	*M. transversalis* Roewer 1912	Punkabari, Darjiling	Roewer (1955)
	10	*M. plebeja* Thorell 1889	Burma (Prome, Minkla)	Roewer (1955)
	11	*M. tristis* Thorell 1889	Burma (Teinzo)	Roewer (1955)
	12	*M. unicolor* Roewer 1912	Orissa, Nepal, Dawna Hills	Roewer (1955)
	13	*M. nigra* Roewer 1955	Burma (Mt. Victoria)	Roewer (1955)
	14	*M. laciniipes* Roewer 1955	Burma (Kambaiti)	Roewer (1955)
	15	*M. peguana* Roewer 1955	Burma (Pegu)	Roewer (1955)
	16	*M. dihita* Roewer 1929	Shan States (Forest of Elephant Hill), Burma (Kambaiti)	Roewer (1955)
	17	*M. impressata* Roewer 1955	Shan States	Roewer (1955)
	18	*M. asperula* Roewer 1955	Shan States	Roewer (1955)
	19	*M. yunnanensis* Roewer 1910	China (Yunnan Province)	Roewer (1955)
	20	*M. similaris* Roewer 1955	China (Yunnan Province)	Roewer (1955)
	21	*M. scabra* Roewer 1912	Tongking, Shan States, Indochina (Khusi Tao), Burma (Pegu)	Roewer (1955)
	22	*M. vittata* Roewer 1910	Sumatra (Padang Distr.)	Roewer (1955)
	23	*M. thienemanni* Roewer 1931	Bali (Kintamani)	Roewer (1955)
	24	*M. cinctipes* Banks 1930	Borneo (Mt. Murud)	Roewer (1955)
	25	*M. nigripes* Banks 1930	Borneo (Mt. Murud)	Roewer (1955)
	26	*M. maculipes* Banks 1930	Borneo (Mt. Murud)	Roewer (1955)
	27	*M. sumatrana* Suzuki 1982	Sumatra	Suzuki (1982)

significant difference concerns the penis. In *M. wangi* and *M. satoi,* the penile shafts have concave sides, while in *M. wangi* the end of the glans is truncated, and in *M. satoi* the end of the glans is tapered (Suzuki 1986: 33, fig. 42B). In *M. grandis* and *M. zhui*, the shafts have parallel sides and are flattened ventrally, while in *M. grandis* the shaft arches dorsally, and in *M. zhui* the shaft is concave dorsally.

Molecular data indicate that *Melanopa grandis* is closely related phylogenetically to *Psathyropus* L. Koeh 1878, *Systenocentrus* Simon 1886, *Marthana* Thorell 1891, and *Gagrellula* Roewer 1910 (Hedin et al. 2012), and these taxa resemble each other in external morphology. However, they are quite different in penile morphology: while Palearctic *Melanopa* laek an alate part (sac), other Palearctic gagrellines (mostly Japanese gagrellines, e.g., *Psathyropus*, *Systenocentrus*, and *Gagrellula*) have a conspicuous alate part (Martens 1987:91, Figs. 1a, b). These morphologies are known as "lanceolate" and "sacculate" in Leiobuninae Bank 1893 (McGhee 1970, 1977). Some other species of sclerosomatids have lanceolate penes; e.g., *Leiobunum calcar* (Wood 1868), *L. vittatum* (Say 1821) (Leiobuninae) (Hedin et al. 2012), and *Homalenotus quadridentatus* (Cuvier 1795) (Sclerosomatinae Simon 1879) (Martens 1978:378–380, Figs. 729, 730). These species do not seem to be closely related to the Palearctic *Melanopa*.

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LITERATURE CITED

Cokendolpher, J.C., N. Tsurusaki, A.L. Tourinho, C.K. Taylor, J. Gruber & R. Pinto-da-Rocha. 2007. Euonoi—Historical systematic synopsis. Pp. 108–114. *In* The Harvestmen: The Biology of Opiliones. (R. Pinto-da-Rocha, G. Maehado & G. Giribet, eds.). Harvard University Press, Cambridge, Massachusetts.

Crawford, R.L. 1992. Catalogue of the genera and type species of the harvestman superfamily Phalangioidea (Arachnida). Burke Museum Contributions in Anthropology and Natural History 8:1–60.

Cuvier, B.G. 1795. Description de deux espèces nouvelles d'inseetes. Magasin Encyclopédique 1:205–207.

Giribet, G. & A.B. Kury. 2007. Phylogeny and Biogeography. Pp. 62–87. *In* The Harvestmen: The Biology of Opiliones. (R. Pinto-da-Rocha, G. Machado & G. Giribet, eds.). Harvard University Press, Cambridge, Massachusetts.

Gritsenko, N.I. 1979a. Новый род сенокосцев (Opiliones, Phalangiinae) из Северного Тянь-Шаня и Западного Алтая. Zoologicheskii Zhurnal 58:264–267.

Gritsenko, N.I. 1979b. Материалы к фауне сенокосцев (Opiliones) Приморского края. Pp. 124–132. *In* Nazemnye chlenistonogie Dal'nego Vostoka. (V.T. Petrashevskaya, ed.). Akademiia Nauk SSSR, Vladivostok.

Ha, M.J., J.Y. Bae, H.Y. Chun & J.P. Kim. 2004. Three new record species of the Order Opiliones (Arthropoda: Arachnida) from Korea. Korean Arachnology 20:53–71.

Hedin, M., N. Tsurusaki, R. Macías-Ordóñez & J.W. Shultz. 2012. Molecular systematics of sclerosomatid harvestmen (Opiliones, Phalangioidea, Sclerosomatidae): geography is better than taxonomy in predicting phylogeny. Molecular Phylogeneties and Evolution 62:224–236.

Hillyard, P.D. & J.H.P. Sankey. 1989. Harvestmen: Keys and notes for the identification of the species. Linnean Society of London, Leiden.

Karsch, F. 1881. Diagnoses Arachnoidarum Japoniae. Berliner Entomologisehe Zeitschrift 25:35–40.

Klimeš, L. 2006. A new *Umbopilio* species from Assam, NE India (Opiliones: Sclerosomatidae: Gagrellinae). Zootaxa 1325:147–156.

Koch, L. 1878. Japanesische Arachniden und Myriapoden. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 27:735–798.

Kury, A.B. 2012. Checklist of valid genera of Opiliones of the World. Museu Nacional/UFRJ website. Online at: http://www.museunacional.ufrj.br/mndi/Aracnologia/checklaniator.htm

Li, S.Q. & D.X. Song. 1993. A revision of Chinese Harvestmen, with a note on their geographical distribution. Scientific Treatise on Systematic and Evolutionary Zoology 2:237–245.

Macías-Ordóñez, R., G. Machado, A. Pérez-González & J. Shultz. 2010. Genitalic Evolution in Opiliones. Pp. 285–306. *In* The Evolution of Primary Sexual Characters in Animals. (J. Leonard & A. Córdoba-Aguilar, eds.). Oxford University Press, New York.

Martens, J. 1978. Spinnentiere, Arachnida: Weberknechte, Opiliones. Pp. 1–464. *In* Die Tierwelt Deutschlands. (K. Senglaub, H.J. Hannemann & H. Schumann, eds.). Fischer Verlag, Jena.

Martens, J. 1986. Die Grossgliederung der Opiliones und die Evolution der Ordnung (Araehnida). Pp. 289–310. *In* Actas del X Congreso Internacional de Aracnologia. (J.A. Barrientos, ed.). Jaca, Spain.

Martens, J. 1987. Opiliones aus dem Nepal-Himalaya. VI. Gagrellinae (Arachnida: Phalangiidae). Courier Forschungsinstitut Senekenberg 93:87–202.

McGhee, C.R. 1970. The sacculate and lanceolate groups of the genus *Leiobunum* (Arachnida: Phalangida, Phalangiidae) in the eastern United States. Unpublished Doctoral Dissertation, Department of Zoology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia.

McGhee, C.R. 1977. The politum group (bulbate species) of *Leiobunum* (Arachnida: Phalangida: Phalangiidae) of North America. Journal of Arachnology 3:151–163.

Redikortsev, V.V. 1936. Materialy k faune Opiliones SSSR. Trudy Zoologiceskogo Instituta Akademija Nauk SSSR 3:33–57.

Roewer, C.F. 1910. Revision der Opiliones Plagiostethi (= Opiliones Palpatores). 1. Teil: Familie der Phalangiidae. (Subfamilien: Gagrellini, Liobunini, Leptobunini). Abhandlungen aus dem Gebiete der Naturwissenschaften in Hamburg 194:1–294.

Roewer, C.F. 1923. Die Weberknechte der Erde. Systematische Bearbeitung der bisher bekannten Opiliones. Gustav Fischer, Jena.

Roewer, C.F. 1954. Indoaustralische Gagrellinae (Opiliones, Arachnidae). Senckenbergiana Biologica 35:237–292.

Roewer, C.F. 1955. Indoaustralische Gagrellinae (Opiliones, Arachnidae). Senckenbergiana Biologica 36:71–121.

Sato, I. & S. Suzuki. 1938. Uber neue Arten der Gagrellinae (Palpatores, Opiliones) aus Japan. Annotationes Zoologicae Japonenses 17:373–387.

Say, T. 1821. An account of the Arachnides of the United States. Journal of the Academy of Natural Sciences of Philadelphia 2:59–82.

Šilhavý, V. 1976. Two new opilionids of the family Leiobunidae from Korea (Arach., Opiliones). Věstník československé Společnosti zoologické 40:296–299.

Simon, E. 1879. Les Arachnides de France. Tome 7. Contenant les ordres des Chernetes, Scorpiones et Opiliones. Librairie Encyclopédique de Roret, Paris.

Simon, E. 1886. Arachnides recueillis par M. A. Pavie (sous-chef du Service des Postes au Cambodge) dans le royaume de Siam, au Cambodge, et en Cochinchine. Actes de la Société Linnéenne de Bordeaux 10:137–166.

Staręga, W. 1965. Einige Weberknechte (Opiliones) aus Nordkorea (Materialien zur Kenntnis der ostasiatischen Weberknechte, V). Annales Zoologici 23:5–14.

Staręga, W. 1972. Revision der Phalangiidae (Opiliones), I. Gattung Bunochelis Roewer, 1923. Annales Zoologici 29:461–471.

Staręga, W. 1978. Katalog der Weberknechte (Opiliones) der Sowjet-Union. Fragmenta Faunistica 23:197–241.

Stoliczka, F. 1869. Contribution towards the knowledge of Indian Arachnoidea. Journal of the Asiatic Society of Bengal 2:201–251.

Suzuki, S. 1960. Arachnida Opiliones. Pp. 22–25. *In* Encyclopaedia Zoologica Illustrated in Colours. (Y.K. Okada & T. Uchida, eds.). Hokuryu-kan, Tokyo.

Suzuki, S. 1963. A new genus of Gagrellinae (Opiliones) from Japan. Annotationes Zoologicae Japonenses 36:97–101.

Suzuki, S. 1965. General statement of the class Arachnida; order Opiliones. Pp. 347–355. *In* New Illustrated Encyclopedia of the Fauna of Japan. (Y.K. Okada & T. Uchida, eds.). Hokuryu-kan, Tokyo.

Suzuki, S. 1966. The phalangids of Himalayan Expedition of Chiba University 1963. Japanese Journal of Zoology 15:115–124.

Suzuki, S. 1972. Geographical variation in *Melanopa grandis* Roewer of East Asia (Arach., Opiliones). Proceedings of the 5th International Congress of Arachnology 1971:65–70.

Suzuki, S. 1973. Opiliones from the South-west Islands, Japan. Journal of Science of the Hiroshima University 24:20KO5–279.

Suzuki, S. 1982. Contributions to the taxonomy and zoogeography of the Opiliones of the Philippines, Bismark and Solomon Islands. With an appendix on some related species from the Moluccas and Sumatra. Steenstrupia 8:181–225.

Suzuki, S. 1985. Revision of five problematical species of Japanese Opiliones. Proceedings of the Japanese Society of Systematic Zoology 30:53–59.

Suzuki, S. 1986. Opilionids of Hiroshima Prefecture (Arachnida). Hibagaku, Journal of the Hiba Society of Natural History 132:7–45.

Suzuki, S. & N. Tsurusaki. 1983. Opilionid fauna of Hokkaido and its adjacent areas. Journal of the Faculty of Science Hokkaido University 23:195–243.

Taylor, C.K. 2009. Revision of the Australian Gagrellinae (Arachnida: Opiliones: Sclerosomatidae), with a description of a new species. Australian Journal of Entomology 48:217–222.

Tchmeris, A.N. 2000. Contribution to the knowledge of the harvestman fauna in the Russian Far East and Eastern Siberia (Arachnida: Opiliones). Arthropoda selecta 9:31–49.

Thorell, T.T.T. 1889. Aracnidi Artrogastri Birmani raccolti da L. Fea nel 1885–1887. Annali del Museo Civico di Storia Naturale di Genova 2 7:521–729.

Thorell, T.T.T. 1891. Opilioni nuovi o poco conosciuti dell'Arcipelago Malese. Annali del Museo Civico di Storia Naturale di Genova 2 10:669–770.

Tourinho-Davis, A.L. 2004. A new genus of Gagrellinae from Brazil, with a comparative study of some of the southernmost tropical and subtropical South American species (Eupnoi, Sclerosomatidae, Gagrellinae). Revista Ibérica de Aracnología 9:157–177.

Tourinho, A.L. & A.B. Kury. 2001. Notes on *Holcobunus* Roewer, 1910 (Arachnida, Opiliones, Sclerosomatidae). Boletim do Museu Nacional: Zoologia 461:1–22.

Tsurusaki, N. 1982. Intersexuality and gynandromorphism in gagrellid harvestmen (Palpatores, Opiliones, Arachnida). Acta arachnologica 31:7–16.

Tsurusaki, N. 2006. Harvestmen of Shimane Prefecture, western Honshu, Japan: An annotated list of species with special reference to geographic variation (Arachnida: Opiliones). Pp. 1–274. *In* Animals and Plants of Shimane Prefecture, New Edition, (Board of the Shimane Meeting of the Japanese Society of Biological Education ed.). 2006, Board of the Shimane Meeting of the Japanese Society of Biological Education, Izumo, Shimane Pref., Japan.

Tsurusaki, N. & S. Hiroyuki. 1991. Opiliones of Fukui prefecture, Central Honshu, Japan. Entomological Journal of Fukui 8:2–20.

Tsurusaki, N., M. Takanashi, N. Nagase & S. Takashi. 2005. Fauna and biogeography of harvestmen (Arachnida: Opiliones) of the Oki Islands, Japan. Acta Arachnologica 54:51–63.

With, C.J. 1903. New and old Phalangiidae from the Indian region. Journal of the Linnean Society of London 28:466–509.

Wood, H.C. 1868. On the Phalangeae of the United States of America. Proceedings of the Essex Institute 6:10–40.

Zhu, M.S. & D.X. Song. 1999. Two species of harvestmen (Arachnida: Opiliones: Phalangidae) from China. Journal of Hebei University 19:159–162.

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Variation in the spiniform macrosetae pattern on the basitarsi of *Diplocentrus tehuacanus* (Scorpiones: Diplocentridae): new characters to diagnose species within the genus

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Abstract. Spiniform macrosetae have been useful as a taxonomic trait in the genus *Diplocentrus*, such as the telotarsal spiniform macrosetae formula widely used to separate species. Basitarsal spiniform macrosetae have been studied in the family Scorpionidae but not in its sister family (Diplocentridae). In this study, we analyzed the variation in the position and number of spiniform macrosetae on the basitarsus of one species of the genus *Diplocentrus*. We found minimal ontogenetic, intersexual and geographical variation within the species. We also compare the pattern found in *Diplocentrus tehuacanus* Hoffmann 1931 to those of two morphologically similar species, and found that the basitarsal macrosetal pattern is also a good, reliable taxonomic character at the interspecific level.

Keywords: Ontogenetic variation, intersexual variation, geographical variation, interspecific variation, diagnostic character

Spiniform setae on scorpion legs have been used as a reliable source of taxonomic information, especially in the superfamily Scorpionoidea Latreille 1802 (Francke 1978; Lamoral 1979; Prendini 2000). For example, species of the family Diplocentridae are partially characterized by the telotarsal spiniform macrosetae formula. This formula (e.g., 4/4: 4/5: 5/5: 6/6) represents the number of spiniform macrosetae present on each face (prolateral/retrolateral) of the ventral aspect of the telotarsus on the four pairs of legs (I: II: III: IV). Basitarsal spiniform macrosetae have been considered only for the family Scorpionidae (Prendini et al. 2003) and have been ignored in the family Diplocentridae.

Recently, the basitarsal spiniform macrosetae pattern for legs III–IV has been used to separate species groups in *Diplocentrus* Peters 1861 (Santibáñez-López et al. 2013) and to diagnose *D. zacatecanus* Hoffmann 1931 (Santibáñez-López & Francke 2013), but no other attempt has been made to analyze its utility as a species-specific diagnostie character, nor as a phylogenetically informative character. In a separate contribution, the basitarsal macrosetal pattern for the genera within the family Diplocentridae has been tested to determine its utility as a generic diagnostic character (Santibáñez-López et al. in prep.).

To study the variation in the position and number of spiniform macrosetae on the ventral face of the basitarsus of the species in this family, we analyzed the degree or extent of intraspeeific variation first on one species: *Diplocentrus tehuacanus* Hoffmann 1931, a species that is widely distributed in central Mexico and is well represented in collections (Fig. 1). In the present contribution, we considered four types of variation: a) individual variation (bilateral symmetry), b) ontogenetic variation (three stages of development), c) sexual dimorphism (males versus females) and d) geographical variation (different populations).

METHODS

Terminology for the leg segmentation follows Couzijn (1976), and for spiniform setae Lamoral (1979), McWest (2009) and slightly modified from Prendini (2000). We consider the spiniform macroseta as stout, blunt seta, spine-like, with a socketed base and usually dark in color.

Spiniform macrosetal pattern on the leg basitarsus.—These setae are found on the ventral face of the basitarsus of the four legs; the arrangement (position and number of setae) is different between them, except for legs III and IV, which present the same pattern (Fig. 2). Macrosetae on the distal margin of the segment are not considered, only those on the ventral face proper. Setae are named according to their relative position on the transverse axis of the ventral face of the basitarsus: p = prolateral side, v = ventral, r = retrolateral; and followed by their position with respect to the longitudinal axis: t = terminal, st = subterminal, m = medial, sb = suprabasal and b = basal. For example, a seta named pt means that it is found on the prolateral side and near the terminal portion of the basitarsus (e.g., Fig. 3). On legs I and II, one spiniform macroseta is also found on the retrolateral face, at the medial portion of the basitarsus (located in the retrolateral face and not in the ventral face; therefore, we use capital R: Rm to designate it; Fig. 3). The presence of the retrolateral median spiniform macroseta on leg II is a diagnostic trait for the genus *Diplocentrus* [the importance of the basitarsal macrosetae for the taxonomy of the family will be presented elsewhere (Santibáñez-López et al. in prep.)].

Observations were made using a stereoscopic microscope, Nikon SMZ 800. All illustrations are ventral views of the corresponding right leg (I, II, III and IV) and the prolateral pedal spur, located in the joint between the basitarsus and the telotarsus, is shown to help the reader understand the relative positions of the macrosetae studied. Illustrations were drawn using the software Adobe Illustrator C3.

Sixty-five specimens from different populations covering a wide range of the geographic distribution of *D. tehuacanus* were studied, including 44 adults (30 males and 14 females), 15 subadults (7 males and 8 females) and 6 juveniles.

In order to analyze the variation in the number and position of the setae present on the basitarsi, we considered the following:

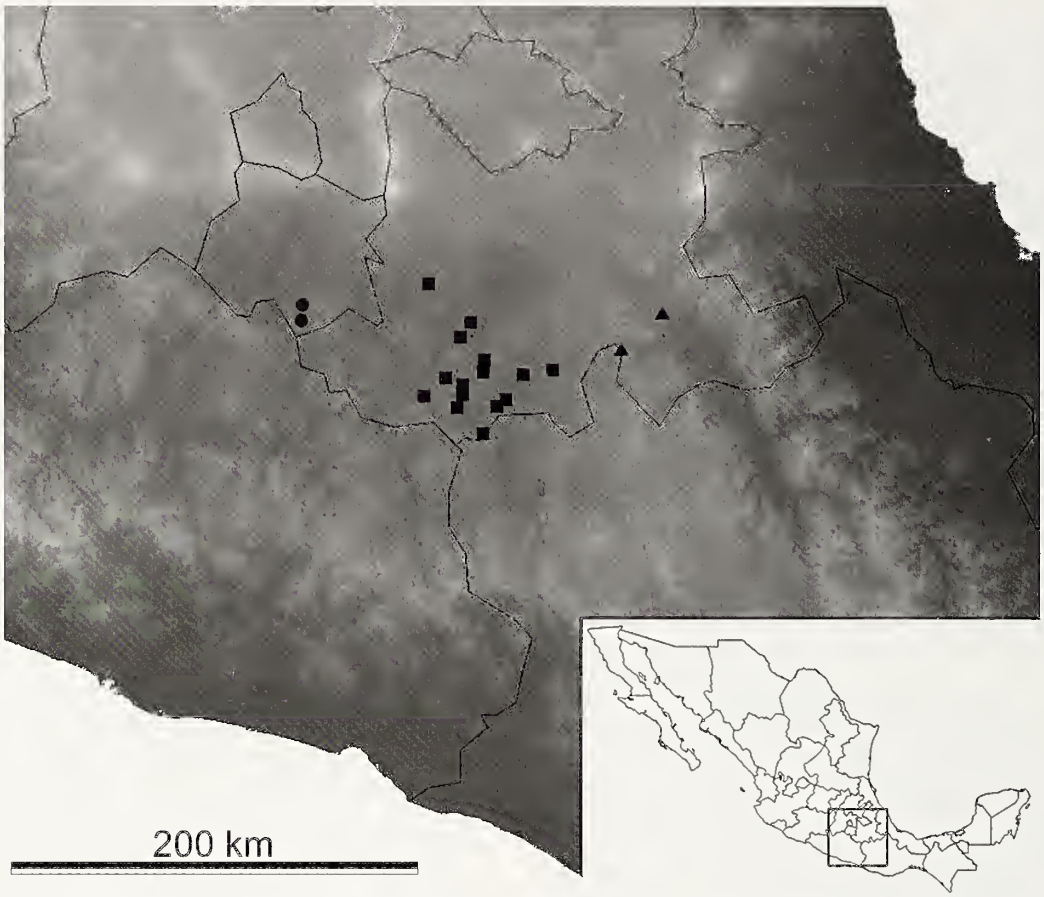

Figure 1.—*Diplocentrus tehuacanus* Hoffmann 1931, known records in central Mexico. Map divided into three regions for analysis of geographical variation in basitarsal macrosetae: Region I (circles), Region II (squares) and Region III (triangles).

a) Individual variation. To determine whether asymmetrical variation within a single specimen existed, we compared the position and number of the macrosetae on both legs. We used (randomly selected) 12 males, 12 females, and 6 juveniles.
b) Ontogenetic variation. To analyze variation in the position and number of the macrosetae between different developmental stages, we compared their arrangement on all adults against the subadults and juveniles.
c) Sexual variation. To determine whether sexual dimorphism in spiniform macrosetal patterns within the species was present, we compared the arrangement of the macrosetae on each leg (I, II, III and IV) in males and females.
d) Geographical variation. Because the range of distribution of the species is wide, we divided the populations available into three geographical sections: those found in the northern range of the distributional area (Region I with 10 specimens), those found in the central range (Region II with 43 specimens), and those found in the southeastern range of the distribution area (Region III with 12 specimens, which includes the type locality; see Fig. 1). We compared the ventral basitarsal spiniform macrosetal pattern on each leg (I, II, III and IV) from each region to each other, to determine whether geographical variation was present.

Finally, we propose a generalized pattern for the species, and compare it against the pattern of two morphologically similar species also found in central Mexico: *Diplocentrus coylei* Fritts & Sissom 1996 and *Diplocentrus longimanus* Santibáñez-López et al. 2011.

Abbreviations of specimen depositories are CNAN – Coleccion Nacional de Aracnidos, Instituto de Biologia, UNAM; CAIMSc – Instituto de Diagnóstico y Referencia Epidemiologicos, Secretaria de Salud, Mexico.

Specimens studied.—*Diplocentrus tehuacanus* Hoffmann 1931: MEXICO, REGION I: *Morelos*, Tlaquiltenango, Huautla 18°26′24″N, 99°01′30″W, 945 m, 3 August 2003, M. Córdova, A. Jaimes and H. Lagunas, 1 ♀, 1 ♂, 2 subadult ♀, 2 juveniles (CNAN-503038); Tlaquiltenango, Quilamula 18°30′37″N, 99°01′11″W, 1070 m, unknown date; M. Córdova and A. Jaimes, 3 ♂, 1 ♀ (CNAN-503213). REGION II: *Puebla*. Acatlán 18°12′12″N, 98°02′55″W, 1180 m, 21 June 2000, V. Vidal, 2 ♂ (CAIMSc-04249); Acatlán, Rancho Nuevo 17°56′41″N, 98°13′16″W, 1220 m, 10 November 2005, unknown collector, 1 ♀ (CAIMSc-04240); Ahuehuetitla 18°12′44″N, 98°13′16″W, 1200 m, 8 January 2003, unknown collector, 2 ♂, 2 ♀, 1 subadult ♂, 1 subadult ♀ (CAIMSc-O4259); Axutla 18°11′21″N, 98°23′24″W, 860 m, 30 September 2004, unknown collector, 2 subadult ♂, 1 subadult ♀ (CAIMSc-04254); Chila de la Sal 18°06′36″N, 98°29′03″W, 940 m, 9 July 2003, unknown collector, 1 ♂, 1 ♀, 1 subadult ♂ (CAIMSc-04271); Chinautla 18°16′03″N, 98°13′11″W, 1200 m, 20 October 2000, unknown collector, 2 ♀ (CAIMSc-04278); Guadalupe 18°05′35″N, 98°07′14″W, 1100 m, 17 April 2006,

Figure 2.—*Diplocentrus tehuacanus* Hoffmann 1931, legs I–III, basitarsus and telotarsus, showing ventral spiniform macrosetae.

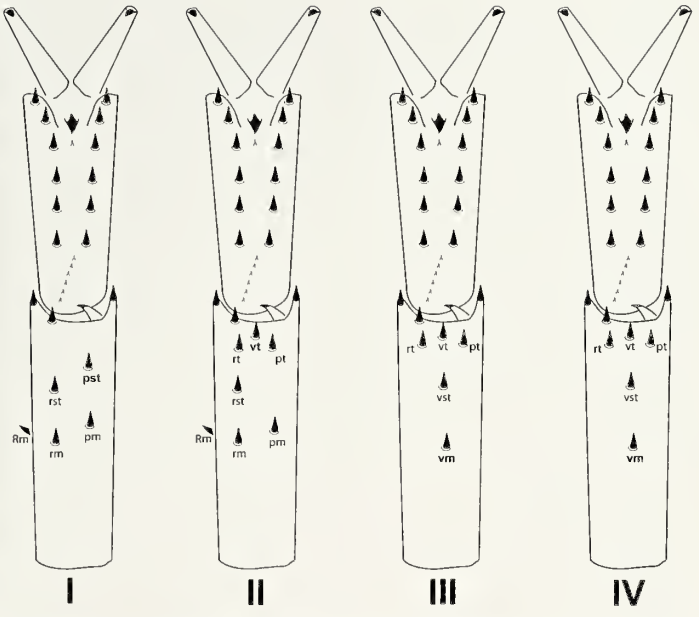

Figure 3.—*Diplocentrus tehuacanus* Hoffmann 1931, basitarsal ventral spiniform macrosetal pattern (differences from the other two species included in this study marked in bold type).

unknown collector, 1 ♂ (CAIMSc-04253); Guadalupe, La Providencia 18°03′46″N, 98°09′53″W, 1060 m, 9 August 2006, unknown collector, 1 ♀ (CAIMSc-04247); Izucar de Matamoros 18°36′10″N, 98°27′55″W, 1280 m, 23 June 2004, unknown collector, 1 ♀, 3 subadult ♂, 1 subadult ♀ (CAIMSc-04245); Piaxtla, Tlaxcoapan 18°09′22″N, 98°18′40″W, 980 m, 1 September 2000, unknown collector, 1 ♂ (CAIMSc-04273); San Jeronimo Xayacatlan 18°13′22″N, 97°54′52″W, 1320 m, 6 March 2006, unknown collector, 1 ♂ (CAIMSc-04241); Tecomatlán, Rancho Nuevo 18°03′27N, 98°20′09″W, 980 m, August 2001, unknown collector, 2 ♂, 2 ♀ (CAIMSc-04246); Tecomatlán, Rancho Nuevo 18°03′27N, 98°20′09″W, 980 m, 13 March 2006, unknown collector, 1 ♀ (CAIMSc-04243); Tecomatlán 18°06′44″N, 98°18′54″W, 920 m, 1 June 2001, F. Martinez, 1 ♂ (CAIMSc-04239); Tehuitzingo, San Francisco de Asís 18°26′12″N, 98°16′45″W, 1060 m, 7 September 2001, unknown collector, 4 ♂, 1 ♀ (CAIMSc-04261); Tehuitzingo, Tuzantlán 18°22′01″N, 98°19′31″W, 1000 m, 11 September 1999, unknown collector, 1 ♂ (CAIMSc-04269); Xicotlán, Coacalco 18°04′18″N, 98°40′05″W, 800 m, 5 June 2001, M. Sanchez, 5 ♂ (CAIMSc-04257). REGION III: *Puebla*, Tehuacán, San Lorenzo (18°28′20″N, 97°26′W, 1660m) 22 January 1964, L. Vazquez, 1 ♂, 3 subadult ♀, 4 juveniles (CNAN-500726); Zapotitlán, San Juan Raya 18°18′58″N, 97°36′54″W, 1840 m, unknown date, unknown collector, 4♂ (CAIMSc-04250).

Diplocentrus coylei Fritts & Sissom 1996: MEXICO: *Guerrero*, El Comal, Buena Vista de Cuellar 18°27′86″N, 99°17′39″W, 1749 m, 13 June 2007, O. Francke et al., 5 ♂, 4 ♀, 1 subadult ♂, 2 subadult ♀, 3 juveniles (CNAN-503262).

Diplocentrus longimanus Santibáñez-López et al., 2011: MEXICO: *Puebla*, Altepexi 18°22′03″N, 97°17′55″W, 1240 m, 16 October 2000, unknown collector, 1 ♂ (CAIMSc-04308); Ahuehuetitla 18°12′44″N, 98°13′16″W, 1200 m, 1 May 2004, unknown collector, 1 ♂ (CAIMSc-O1147); Chila de la Sal 18°06′36″N, 98°29′03″W, 940 m, 19 June 2000, unknown collector, 1 ♀ (CAIMSc-04271); Piaxtla, Tlaxcoapan 18°09′22″N, 98°18′40″W, 980 m, 1 September 2000, unknown collector, 2 ♂ and 1 ♂ subadult (CAIMSc-04306); Tehuitzingo, Tejalpa 18°21′39″N, 98°21′37″W, 960 m, 6 Deeember 2001, E. Bello, 1 ♂ (CAIMSc-04269); Tulcingo, Aguacatitlán 17°58′43″N, 98°20′02″W, 1100 m, 4 September 2003, M.A. Sanchez and F. Santos R, 1 ♂ (CAIMSc-04297); Xicotlán 18°03′34″N, 98°31′32″W, 1260 m, 17 October 2001, unknown collector, 1 ♂ (CAIMSc-04257).

RESULTS

The spiniform macrosetal pattern was more variable on leg I than on the others, followed by leg II. The basitarsal spiniform macrosetal pattern for *Diplocentrus tehuacanus* is as follows (see also Fig. 3):

Leg I. Two subterminal spiniform macrosetae (pst and rst) and two median spiniform macrosetae (pm and rm) are found. The presence of a ventral terminal macroseta (vt) was observed in 11 of the 65 specimens, and it was always asymmetrical (present on one side and absent on the other; Table 1) and is not considered part of the generalized species-specifie pattern. A retrolateral terminal macroseta (rt) was found on 11 specimens; on 5 of them asymmetrically (present on one side and absent on the other) and on 6 specimens present on both legs; it is nonetheless not considered part of the species-specific pattern because it is missing in the majority of the specimens (Table 1). A retrolateral median spiniform macroseta (Rm) is present on all specimens.

Leg II. Three terminal spiniform macrosetae are found (pt, vt and rt), one subterminal (rst) and two median spiniform macrosetae (pm and rm) are present. On this leg, we found only one case of asymmetry, involving macroseta rm (Table 1). On the retrolateral surface, the median spiniform macroseta (Rm) is present on all specimens.

Legs III and IV. These two legs share the same basitarsal macrosetal pattern: Three terminals (pt, vt and rt), one subterminal (vst) and one median (vm) spiniform macrosetae

Table 1.—Variation in the position and number of the basitarsal spiniform macrosetae on legs I–IV. 0 = absence, 1 = presence; x = leg missing. All spiniform macrosetae are located on the ventral face of the basitarsus, except as noted: pt = prolateral terminal, rt = retrolateral terminal, vt = ventral terminal, pst = prolateral subterminal, rst = retrolateral subterminal, vst = ventral subterminal, pm = prolateral median, rm = retrolateral median, vm = ventral median, Rm = retrolateral median on retrolateral face.

			LEG I							LEG II							LEG III					LEG IV				
Sex	Stage	Leg	vt	rt	pst	rst	pm	rm	Rm	pt	rt	Vt	rst	Pm	rm	Rm	pt	vt	rt	vst	vm	pt	vt	rt	vst	vm
♀	adult	left	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♀	adult	left	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♀	adult	left	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♂	adult	left	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♂	adult	left	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♂	subad	left	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♂	subad	left	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♂	subad	left	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♂	subad	left	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♀	subad	left	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♀	adult	left	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♂	adult	left	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♂	adult	left	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♂	adult	left	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♂	adult	left	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1
♀	adult	left	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♂	adult	left	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♀	adult	left	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1

Table 1.—Continued.

			LEG I							LEG II							LEG III					LEG IV				
Sex	Stage	Leg	vt	rt	pst	rst	pm	rm	Rm	pt	rt	Vt	rst	Pm	rm	Rm	pt	vt	rt	vst	vm	pt	vt	rt	vst	vm
♀	adult	left	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♀	subad	left	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
?	juv	left	0	0	1	1	1	1	1	x	x	x	x	x	x	x	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	x	x	x	x	x	x	x	1	1	1	1	1	1	1	1	1	1
?	juv	left	x	x	x	x	x	x	x	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♂	adult	left	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♀	subad	left	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♀	subad	left	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
♀	subad	left	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
?	juv	left	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
?	juv	left	x	x	x	x	x	x	x	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
?	juv	left	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
?	juv	left	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
		right	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 2.—Ontogenetic variation (noted in bold type, or laek thereof) on the spiniform macrosetae on the ventral (and the retrolateral) face of legs I–IV. *n* = sample size (one juvenile missing both legs II); pt = prolateral terminal, rt = retrolateral terminal, vt = ventrolateral terminal, pst = prolateral subterminal, rst = retrolateral subterminal, vst = ventral subterminal, pm = prolateral medial, rm = retrolateral medial, vm = ventral medial, Rm = Retrolateral medial on retrolateral face; - = inapplicable. On all juveniles, instead of a spiniform macroseta, a stunted macroseta was present on the retrolateral face.

Leg	Stage	*n*	pt	Rt	vt	pst	rst	vst	pm	rm	vm	Rm
I	Adults	88	-	28	12	86	85	-	86	74	-	88
	Subadults	30	-	**6**	**5**	30	30	-	30	30	-	30
	juveniles	12	-	**0**	**0**	10	10	-	10	10	-	**10***
II	Adults	88	88	88	88	-	86	-	86	80	-	88
	Subadults	30	29	29	29	-	29	-	29	29	-	30
	juveniles	10	10	10	10	-	10	-	10	10	-	10
III	Adults	88	88	88	88	-	-	88	-	-	87	-
	Subadults	30	30	30	30	-	-	30	-	-	30	-
	juveniles	12	12	12	12	-	-	12	-	-	12	-
IV	Adults	88	87	88	87	-	-	87	-	-	88	-
	Subadults	29	29	29	29	-	-	29	-	-	29	-
	juveniles	12	12	12	12	-	-	12	-	-	12	-

Table 3.—Sexual variation on the presence and counts of spiniform macrosetae on the ventral (and retrolateral) face of legs I–IV: *n* = sample size; pt = prolateral terminarl, rt = retrolateral terminal, vt = ventrolateral terminal, pst = prolateral subterminal, rst = retrolateral subterminal, vst = ventral subterminal, pm = prolateral medial, rm = retrolateral medial, vm = ventral medial, Rm = Retrolateral medial on retrolateral face; - = inapplicable.

Leg	Stage	Sex	*n*	pt	rt	vt	pst	rst	vst	pm	rm	vm	Rm
I	adult	♂	74	-	21	8	72	71	-	72	62	-	74
	adult	♀	44	-	13	9	44	44	-	44	42	-	44
II	adult	♂	74	74	74	74	-	74	-	73	66	-	74
	adult	♀	44	44	44	44	-	44	-	44	44	-	44
III	adult	♂	74	74	74	74	-	-	74	-	-	74	-
	adult	♀	44	44	44	44	-	-	44	-	-	43	-
IV	adult	♂	73	73	73	72	-	-	73	-	-	73	-
	adult	♀	44	43	43	44	-	-	43	-	-	44	-

Table 4.—Analysis of geographical variation on the spiniform macrosetae on the ventral face of legs I–IV. *n* = sample size; pt = prolateral terminal, rt = retrolateral terminal, vt = ventrolateral terminal, pst = prolateral subterminal, rst = retrolateral subterminal, vst = ventral subterminal, pm = prolateral medial, rm = retrolateral medial, vm = ventral medial, Rm = Retrolateral medial on retrolateral face, Rt = Retrolateral terminal on retrolateral face; - = inapplicable.

Leg	Region	*n*	pt	Rt	vt	pst	rst	vst	pm	rm	vm	Rm
I	I	20	-	10	7	18	18	-	18	19	-	20
	II	86	-	24	10	85	84	-	84	73	-	86
	III	24	-	0	0	23	23	-	24	22	-	22
II	I	18	18	18	18	-	18	-	18	18	-	18
	II	86	86	86	86	-	86	-	86	78	-	86
	III	24	24	24	24	-	24	-	23	23	-	24
III	I	20	20	20	20	-	-	20	-	-	20	-
	II	86	86	86	86	-	-	86	-	-	85	-
	III	24	24	24	24	-	-	24	-	-	24	-
IV	I	20	20	20	20	-	-	20	-	-	20	-
	II	85	84	85	84	-	-	84	-	-	85	-
	III	24	24	24	24	-	-	24	-	-	24	-

Table 5.—Interspecific variation on the spiniform macrosetae on the basitarsus of legs I–IV in three species of *Diplocentrus* Peters 1861 (differences highlighted in bold type): n = sample size; pt = prolateral terminal, rt = retrolateral terminal, vt = ventrolateral terminal, pst = prolateral subterminal, rst = retrolateral subterminal, vst = ventral subterminal, pm = prolateral medial, rm = retrolateral medial, vm = ventral medial, rsb = retrolateral suprabasal, Rm = Retrolateral medial on retrolateral face; - = inapplicable.

Leg	Species	*n*	pt	rt	vt	pst	rst	vst	pm	rm	vm	rsb	Rm
I	*D. tehuacanus*	130	-	34	17	**126**	125	-	126	114	-	-	128
	D. longimanus	20	**20**	18	1	-	20	-	20	20	-	-	18
	D. coylei	30	**28**	-	-	-	30	-	20	28	-	-	30
II	*D. tehuacanus*	128	128	128	**128**	-	128	-	127	**119**	-	-	128
	D. longimanus	20	18	18	-	**18**	18	-	18	-	-	-	18
	D. coylei	30	30	30	**30**	-	29	-	6	-	-	**24**	30
III	*D. tehuacanus*	130	130	130	130	-	-	130	-	-	**129**	-	-
	D. longimanus	20	20	20	20	-	**20**	20	-	-	**20**	-	-
	D. coylei	30	28	28	28	-	2	28	-	-	**2**	-	-
IV	*D. tehuacanus*	129	128	128	128	-	-	128	-	-	**129**	-	-
	D. longimanus	20	20	20	20	-	**20**	20	-	-	**20**	-	-
	D. coylei	30	28	28	28	-	1	28	-	-	**4**	-	-

are found on these legs. A single case of asymmetry involving macroseta pt on leg IV was observed (Table 1).

Variation.—

A) Individual variation. From the sample used in this study, only 13 legs out of 236 studied (30 specimens × 8 legs = 240, less 4 missing legs) showed asymmetry: 11 (4.7%) on leg I (6 on macrosetae vt and 5 on rt); one (0.4%) on leg II (macroseta rm) and one (0.4%) on leg IV (macroseta pt). Six specimens out of 30 (20%) possessed macroseta rt symmetrically on both legs I, and as mentioned above five had it asymmetrically on the same legs I.

B) Ontogenetic variation. Leg I. Seven adults (4 males and 3 females) and 2 subadults (1 male and 1 female) presented macroseta vt, which was absent in all juveniles; 15 adults and 4 subadults presented rt, which was also absent in all juveniles. No differences in the number or the pattern of spiniform macrosetae among age groups were found on the other legs (see Table 2).

C) Sexual variation. No differences in number or pattern of spiniform macrosetae were observed between males and females, although both sexes had a low propensity to present one extra macroseta (either vt or rt) on leg I (as indicated above). No differences between sexes were found on the other legs (see Table 3).

D) Geographical variation. Regions I and II had eight out of 53 specimens (15.1%) with vt and in 19 specimens (35.9%) rt on leg I. The 12 specimens from region III had no extra macroseta on leg I. No other differences were found in the other legs (see Table 4).

Thus the generalized basitarsal spiniform macrosetae formula for *D. tehuacanus* is Leg I with five: pst, rst, pm, rm

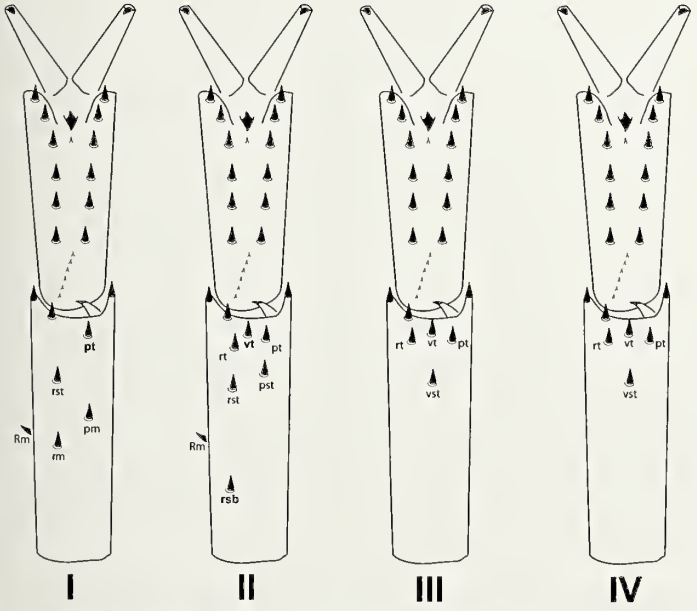

Figure 4.—*Diplocentrus coylei* Fritts and Sissom 1996, basitarsal ventral spiniform macrosetal pattern (differences from the other two species included in this study marked in bold type).

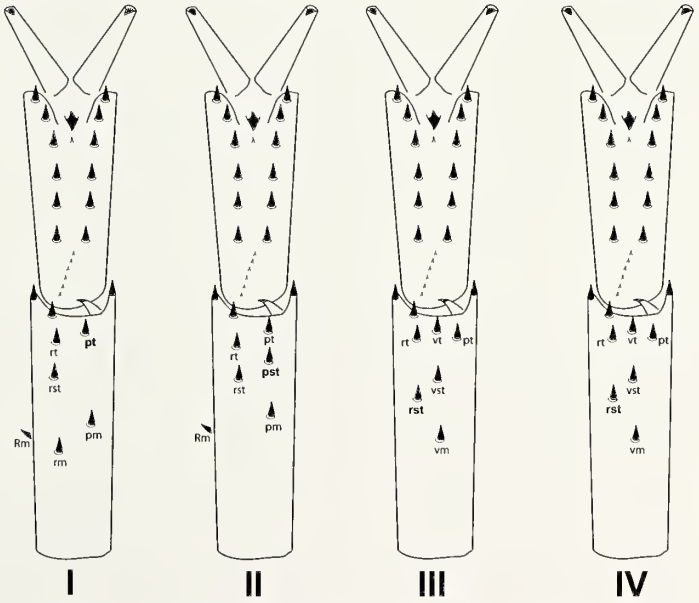

Figure 5.—*Diplocentrus longimanus* Santibáñez-López et al. 2011, basitarsal ventral spiniform macrosetal pattern (differences from the other two species included in this study marked in bold type).

and Rm; Leg II with seven: pt, vt, rt, rst, pm, rm and Rm. Legs III–IV with five: pt, vt, rt, vst and vm (Fig. 3).

Basitarsal spiniform macrosetal formula as a diagnostic species-specific character in the genus *Diplocentrus* Peters 1861.—We compared the pattern found on *D. tehuacanus* against the patterns found on two morphologically similar species: *Diplocentrus longimanus* and *Diplocentrus coylei*. Differences between the patterns are as follows (see also Table 5 and Figs. 3–5):

Leg I. The three species share the presence of macrosetae rst, pm, rm, and Rm, but they differ as follows: *D. longimanus* and *D. coylei* present pt, whereas on *D. tehuacanus* that macroseta is absent; *D. longimanus* presents rt, which is absent on the other two species; and *D. tehuacanus* presents pst, which is absent on the other two species.

Leg II. The presence of macrosetae pt, rt, rst and Rm is common to the three species, but their differences are: *D. coylei* and *D. tehuacanus* present vt, which is absent on *D. longimanus*; *D. longimanus* and *D. tehuacanus* present pm, but it is absent on *D. coylei*; pst is present only on *D. longimanus*, rsb (retrolateral suprabasal) is present only on *D. coylei* and rm is present only on *D. tehuacanus*.

Legs III–IV. The patterns for the three species share the three terminal spiniform macrosetae (pt, vt and rt); they also share the presence of vst, but they differ in the presence of rst (only on *D. longimanus*) and the presence of vm (on *D. longimanus* and *D. tehuacanus*).

CONCLUSIONS

The basitarsal spiniform macrosetal pattern on each of the four legs of species of the genus *Diplocentrus* is rather invariable, showing minimal bilateral asymmetry, predictable ontogenetic changes, lacking sexual dimorphism and presenting minimal geographic variation. Furthermore, there are reliable differences in the basitarsal macrosetal patterns among the three species analyzed. Thus we consider that it is a species-specific diagnostic character and strongly recommend that this pattern be noted on all future descriptions, along with the telotarsal count of spiniform macrosetae.

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LITERATURE CITED

Couzijn, H.W.C. 1976. Functional anatomy of the walking-legs of Scorpionida with remarks on terminology and homologization of leg segments. Netherlands Journal of Zoology 26:453–501.

Francke, O.F. 1978. Systematic revision of diplocentrid scorpions from circum-Caribbean lands. Special Publications of Texas Tech University 14:1–92.

Lamoral, B.H. 1979. The scorpions of Namibia (Arachnida: Scorpionida). Annals of the Natal Museum 23:497–784.

McWest, K. 2009. Tarsal spinules and setae of vaejovid scorpions (Scorpiones: Vaejovidae). Zootaxa 2001:1–126.

Prendini, L. 2000. Phylogeny and classification of the Superfamily Scorpionoidea Latrielle 1802 (Chelicerata, Scorpiones): an exemplar approach. Cladistics 16:1–78.

Prendini, L., T. Crowe & W. Wheeler. 2003. Systematics and biogeography of the family Scorpionidae (Chelicerata: Scorpiones), with a discussion on phylogenetic methods. Invertebrate Systematics 17:185–259.

Santibáñez-López, C.E. & O.F. Francke. 2013. Redescription of *Diplocentrus zacatecanus* (Scorpiones: Diplocentridae) and limitations of the hemispermatophore as a diagnostic trait for genus *Diplocentrus*. Journal of Arachnology 41:1–10.

Santibáñez-López, C.E., O.F. Francke & L. Prendini. 2013. Systematics of the *keyserlingii* group of the genus *Diplocentrus* Peters 1861 (Scorpiones: Diplocentridae), with descriptions of three new species from Oaxaca, Mexico. American Museum Novitates 3777:1–47.

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Synonymy of four *Pardosa* species (Araneae: Lycosidae) undiagnosable without geography

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Abstract. We examined a group of seven morphologically similar species of the genus *Pardosa* to determine the reliability of morphological identification characters independently of additional specimen data, such as habitat and geography. Of the seven, four shared diagnostic character states with other species. These four species have areas of both sympatric and allopatric distribution. Specimens collected from allopatrie areas, thus expected to contain only one species, were identified using only the morphology of the specimens, keeping the locality data hidden, and the reliability of the identifications was assessed. Identifications of the allopatric specimens resulted in a 32% success rate, indicating that the sole use of morphological characters did not work well for identification in this group. Reliance on geographical data to direct an identification would likely result in identification errors in areas of sympatry. As a result we conclude *Pardosa tristis* (Thorell 1877), *P. prosaica* Chamberlin and Ivie 1947 and *P. dromaea* (Thorell 1877), are new synonyms of *Pardosa groenlandica* (Thorell 1872).

Keywords: Taxonomy, synonymy, label data

Taxonomic identification remains one of the most challenging aspects of the biological investigation of many species-rich taxa. Although molecular tools are seeing greater use, for many, morphology is the primary tool used to identify animal species, often in conjunetion with other data such as habitat, geographical, or behavioral information (Packer et al. 2009). However, morphological differences are minor or difficult to discern for some taxa, requiring greater reliance on these other data types for correct identification. Reliance on such data is a questionable taxonomic practice, in which information not obtainable from the specimen itself is required for identification.

One such group of species can be found in the lycosid genus *Pardosa.* The seven species here defined as the *Pardosa groenlandica* species complex – *P. groenlandica* (Thorell 1872), *P. prosaica* Chamberlin & Ivie 1947, *P. tristis* (Thorell 1877), *P. dromaea* (Thorell 1877), *P. lowriei* Kronestedt 1975, *P. albomaculata* Emerton 1885 and *P. bucklei* Kronestedt 1975 – are all so morphologically similar that they were synonymized under *P. groenlandica* at one point or another in their taxonomic histories (Emerton 1894; Roewer 1955; Kronestedt 1975; Dondale & Redner 1990). Additionally, they all share similar geographical ranges, being found across the northern hemisphere from Iceland west to Russia above 32° latitude; each is sympatric with at least one other member of the species complex in a portion of its range. All seven are listed as valid species by Platnick (2013) based on the morphological taxonomic work of Kronestedt (1975), Dondale & Redner (1990), Dondale (1999) and Vogel (2004). The species group is part of the *modica* group of *Pardosa,* one of the most speciose genera of wolf spiders, and five of the members had been previously revised as a subgroup by Dondale (1999). Because of these attributes, these species make an excellent group to test the reliability of identifications made using only morphological diagnostic characters.

METHODS

Fresh specimens were predominantly collected from May through August 2009 across western North America (Fig. 1). In all, 175 adult spiders — 2 *P. albomaculata*, 5 *P. bucklei*, 8 *P. dromaea*, 67 *P. groenlandica*, 8 *P. lowriei*, 30 *P. prosaica*, and 55 *P. tristis* — were collected, preserved in 100% ethanol and stored at −20°C for future molecular work. Specimens have been deposited in the University of Alaska Museum (UAM) Insect Collection (http://arctos.database.museum/saved/Pardosa-Slowik) except for several specimens provided on loan by R.J. Adams (personal collection), Susan Wise-Eagle (personal collection), Gerry Blagoev (University of Ontario, Guelph), and Buzz Morrison [Denver Museum of Nature and Science (DMNS)]. To ensure correct identification of fresh specimens, a voucher set of specimens used in Dondale's sub-group revision (Dondale 1999) was provided by Charles Dondale via the Canadian National Collection (CNC), which consists of 15 *P. groenlandica*, 8 *P. dromaea*, 10 *P. bucklei*, 9 *P. tristis*, and 16 *P. prosaica.* Scanning electron micrographs of these CNC voucher specimens were taken using an ISI-SR50 mieroscope for aid in identification. Additionally, specimens from the DMNS arachnid collection and the University of Alaska Museum Insect Collection were examined. These included specimens identified by B.R. Vogel, C.D. Dondale, T. Kronestedt, D.J. Buckle, W.J. Gertsch, H.K. Wallace, and the first author. Specifically, attention was paid to the characters used in the original descriptions and in more recent taxonomic works by Kronestedt (1975), Dondale & Redner (1990), Dondale (1999) and Vogel (2004). Additionally, identification discussions were had with T. Kronestedt, C.D. Dondale and B.R. Vogel (J. Slowik pers. comm.).

To evaluate the consistency of the published characters for identification, species descriptions of each of the seven species (Kronestedt 1975; Dondale & Redner 1990; Dondale 1999; Vogel 2004) were examined for diagnostic characters that could be used to identify a species without additional habitat, geographical or behavioral data. To test the utility of shared morphological characters (Table 1), newly collected specimens were chosen that could be positively identified based on geography (from regions lacking sympatry with other species group members) and habitat alone. In all, 58 specimens were chosen randomly for a blind identification analysis in which attempts were made at identification using only the published characters in Dondale (1999) and Vogel (2004), keeping the location and habitat information hidden. The percentage of

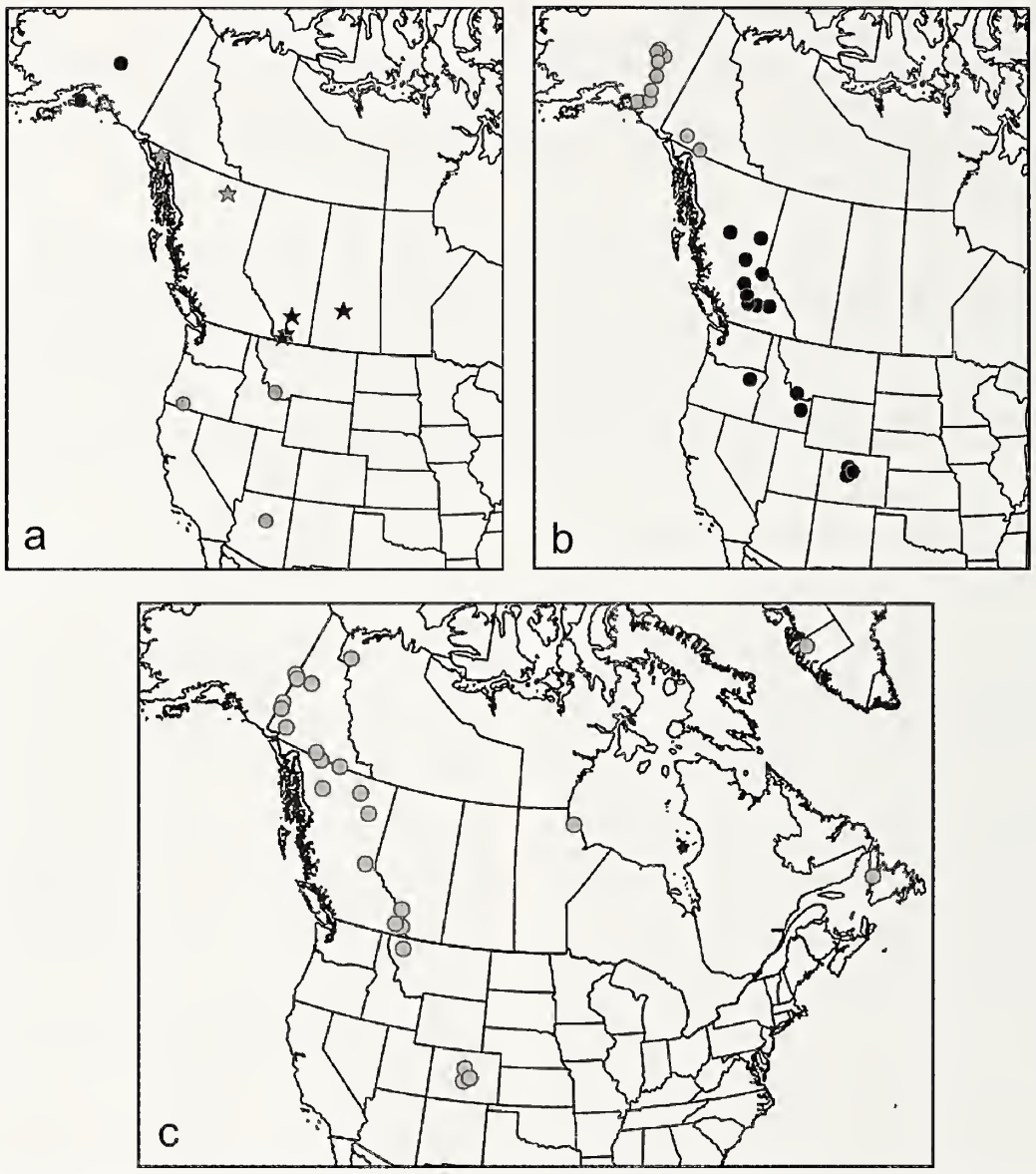

Figure 1.—Collection localities of *Pardosa groenlandica* species complex specimens used in this study. a–dark circles = *P. albomaculata,* light circles = *P. bucklei,* dark stars = *P. dromaea,* light stars = *P. lowriei*; b–dark circles = *P. tristis,* light circles = *P. prosaica*; c–light circles = *P. groenlandica.*

correct identifications was calculated and notes on the identifications were made.

To ensure that the diagnostic characters of these species were properly understood, we added our 58 blind identification specimens to 23 CNC voucher specimens (9 *P. dromaea*, 10 *P. bucklei*, and 4 *P. prosaica*) to replicate the morphometric analysis in Dondale (1999). Measurements on the 81 total specimens included carapace width, carapace length and the *plq* ratio of the epigyna, in which *p* is the length from the anterior end of the median septum (MS) to the atrial sclerite, and *q* is the total length of the MS (Dondale 1999). These new data were compared to Dondale's results using a student's *t*-test for the average of each character. The differences in the means of new data for these characters were compared using an ANOVA, as done in Dondale (1999). If our results matched those of Dondale (1999), this would confirm that we were correctly interpreting and using these diagnostic characters.

RESULTS

Using only the morphological charaeters provided in Kronestedt (1975), Dondale and Redner 1990, Dondale (1999) and Vogel (2004), three species of the *Pardosa groenlandica* species complex could be reliably identified. Both *P. albomaculata* and *P. lowriei* could by identified by the distinctive shape of their conductors and epigyna, particularly the shape of the atria, atrial sclerites, and medium septa (see Kronestedt 1975, Figs. 2–6). The other species all share the distinctive flat conductor tip identified by Dondale (1999) as a character of the *groenlandica* subgroup. *Pardosa bucklei* could be correctly identified using the distinctive thick embolus and the shape of the atrial sclerites, atrium, and MS relative to the atrium. Additionally, *P. bucklei* has a significantly smaller epigynum ($P < 0.0001$; $df = 4, 42$; $F = 10.37$), ranging from 0.60–0.73 mm in length compared to 0.82–1.08 mm for all

Table 1.—Comparison of published diagnostic character groups used for species identification. A "N" indicates that that character state is shared with the species with whom it shares its geographic range.

	Diagnostic embolus	Diagnostic RPTA	Diagnostic MS	Diagnostic atrium	Diagnostic atrial sclerites	Diagnostic size	Species habitat overlaps
P. albomaculata	Y	Y	N	Y	Y	N	*P. groenlandica*
P. lowriei	Y	Y	N	Y	Y	Y	*P. groenlandica, P. prosaica*
P. bucklei	Y	N	N	Y	Y	Y	*P. tristis, P. dromaea*
P. groenlandica	N	N	N	N	N	N	All but *P. bucklei*
P. tristis	N	N	N	N	N	N	*P. groenlandica, P. dromaea*
P. prosaica	N	N	N	N	N	N	*P. groenlandica, P. lowriei*
P. dromaea	N	N	N	N	N	Y	*P. groenlandica, P. tristis*

other species. This species showed little genitalic variation in specimens examined across its range. Additionally, *P. bucklei* is a smaller species and is generally found in a grassy or debris-filled habitat adjacent to water (Dondale 1999; J. Slowik pers. obs., B. Vogel pers. comm.), whereas other *groenlandica* species complex members prefer large scree or cobble areas (Dondale 1999; Vogel 2004, C. D. Dondale pers. comm.; B. R. Vogel pers. comm.; J. Slowik pers. obs.).

The other four members of the species complex (*P. groenlandica, P. tristis, P. prosaica* and *P. dromaea*) were found to lack distinctive morphological characters for reliable identification (Table 1). Results of the blind identifications involving these four species resulted in 43% (25 of 58 specimens) being incorrectly identified using the published morphological characters alone (Dondale 1999; Vogel 2004). Because multiple characters are used for identifieation, 24% (14 of 58 specimens) were found to possess characters from two or three possible species. These specimens could not be identified confidently to a single species. However, of the potential species that these specimens could be, one of them had to be the correct species. Thus, if a determination had to be made, there was a 33–50% possibility that it would have been correct. The remaining 32% (19 of 58 specimens) were correctly identified based on the published characters for identification without the use of geographic or habitat information.

In partieular, the shape of the retrolateral process of the terminal apophysis (RPTA, Fig. 2), which was mentioned as a useful character for species identification of the subgroup by Dondale (1999), was difficult to use and produced inconsistent results. Dissection of the palp is required to observe the RPTA, and damage to the RPTA may occur. Additionally, a lot of variation was seen in the RPTA shape within males from a single population (Mt. Evans, Colorado). A RPTA shape (Fig. 2, *P. tristis*) not mentioned in Dondale was found in several specimens of *P. tristis* from Kamloops and Prince George, British Columbia, and one specimen from Mt. Evans, Colorado. The RPTA shape does not appear to conform to

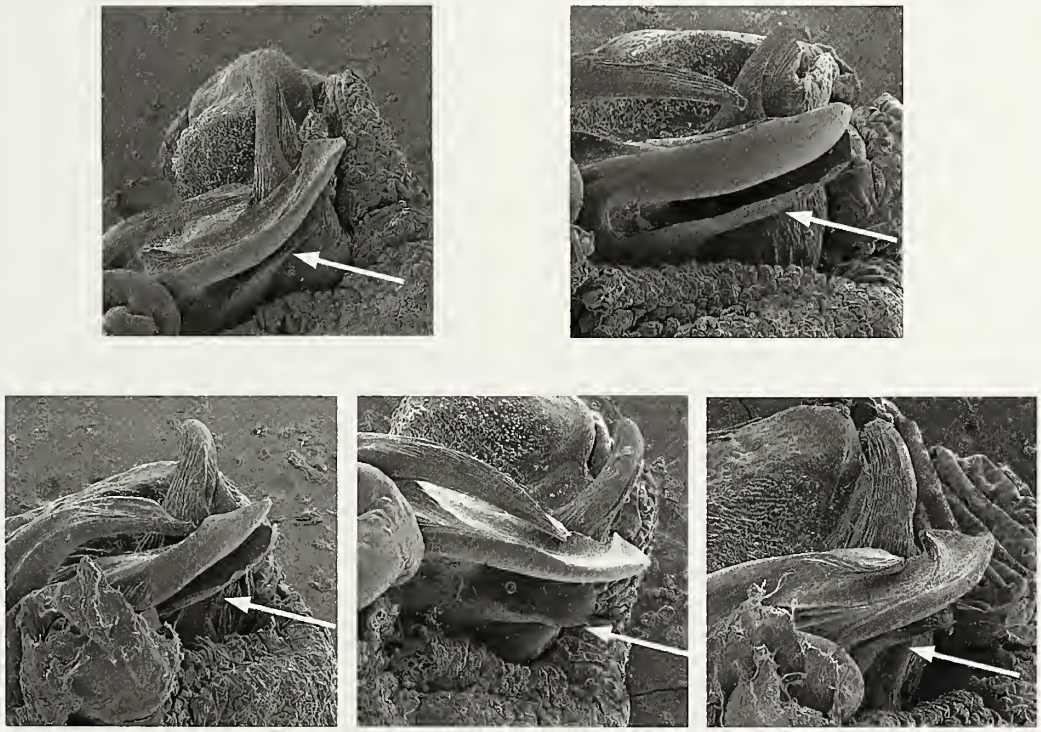

Figure 2.—Scanning electron micrographs of *Pardosa* palpal apical division. Clockwise from upper left; *P. groenlandica, P. tristis, P. dromaea, P. prosaica* and *P. bucklei*. Images 130 × except for *P. bucklei* 190 ×. Arrows point to retrolateral process of the terminal apophysis (RPTA).

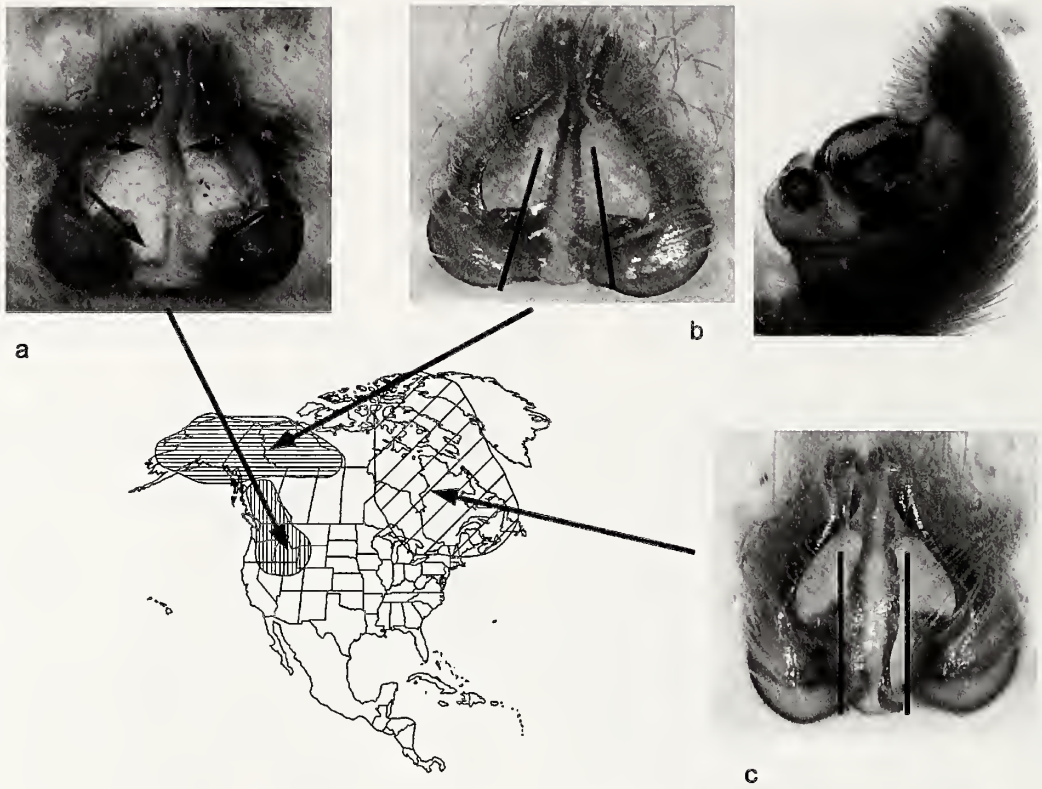

Figure 3.—Morphology and geographic distribution of three *Pardosa groenlandica* species. a–*Pardosa tristis*, inverted T shaped median septum (MS), arrows point to narrow anterior and posterior regions. b–*P. prosaica*, left image - urn shaped MS, lines emphasize widening of MS posteriorly; right image - palp, retrolateral view, arrow points to constriction on interior edge of the embolus. c–*P. groenlandica,* lines emphasize parallel shape of MS lateral edges.

clearly distinct shape categories, but rather appears variable within populations and species.

In the species descriptions for the four species (Dondale 1999; Vogel 2004) the MS shape and sizes of the atria are presented as useful for species identification. Dondale (1999) described three geographic variants based on the shape of the MS, which represented the 32% of our correct identifications in the blind trial. These are an inverted T shape, a bottle shape, and an urn shape with a constricted anterior neck (Fig. 3). The inverted T-shape MS variants are found west of the Rocky Mountains from New Mexico north to British Columbia in the Great Basin and deseribed as *P. tristis* by Dondale (1999). They may be characterized by a long, narrow MS abruptly widening in the posterior region, with the posterior edge often being almost flat. The urn-shaped MS variants were found in Alaska extending east into the Yukon, and were described as *P. prosaica* by Dondale (1999). This variant may be characterized by a narrow anterior region widening into a curved arc along the lateral edge, with a curved posterior edge. The size of the posterior MS expansion was variable. Male specimens from Alaska and Yukon also had a constriction on the interior edge of the embolus (Fig. 3). However, females collected in eastern Yukon and northern British Columbia with urn-shaped median septa were collected with males that did not have the constricted embolus. It would appear that the distribution of urn-shaped median septa extends beyond that of the constricted embolus. The bottle-shaped MS variant was found in specimens from Newfoundland and Greenland and was deseribed as *P. groenlandica* by Dondale (1999). This form is characterized by a relatively wide anterior region, widening somewhat then extending posteriorly and creating almost parallel lateral edges of the MS. These geographie variants were often collected from populations in regions that were supposed to have only one species, which also had individuals with MS shapes not fitting one of the three previously described shapes.

A fourth shape, the "A" shape, was described as being found in both *P. tristis* and *P. prosaica* by Dondale (1999: Fig. 4). This shape did not have a distinct distribution trend and was one source of error in five of the identifications. Misinterpretation of the urn shape resulted in the incorrect identification of eleven specimens, due largely to the constriction of the anterior MS region (Table 2).

The majority of specimens had MS shapes that were a conglomeration of the four described shapes and did not present geographic patterns tied to MS morphology. Figure 4 shows an example, with a narrow anterior region widening similarly to a bottle-shaped MS, a gradual curving lateral edge similar to an urn-shaped MS and a flat posterior edge similar to an "A" or inverted T-shaped MS. This specimen could not be identified without recourse to its collection locality data. Other specimens had a narrow MS that failed to expand posteriorly at all (Somers Beach, Montana, $n = 2$). Specimens expressing median septa outside of the published descriptions were often collected syntopically, in regions that were supposed to have one species, with specimens that did present one of the four described shapes, demonstrating considerable within-population variation in this character.

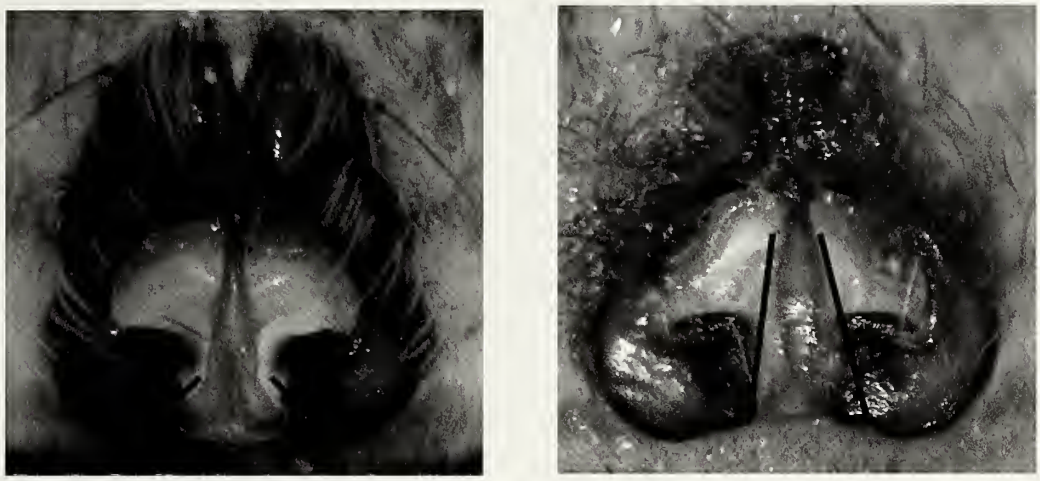

Figure 4.—Additional median septum (MS) shapes of *Pardosa groenlandica* species complex specimens. a–"A" shaped MS, lines emphasize abrupt posterior widening of MS. b–example of MS showing a conglomeration of characters, arrows point to wider anterior region similar to a bottle shaped MS, lines emphasize posterior swelling of MS similar to an urn shaped MS.

Comparison of the morphometric data with those of Dondale (1999) was only significantly different for one character, male *P. bucklei* carapace length (Fig. 5, $P = 0.0039$, $df=8$, $t = 4.01$). Our results showed *P. bucklei* to be significantly different from all other species included in the *groenlandica* subgroup for all measured characters (Table 3, $P < 0.05$). *Pardosa dromaea* was found to be significantly smaller for all characters except for female carapace length ($P < 0.05$). These data are in general agreement with Dondale's results and led to the same general conclusions; that *P. bucklei* and *P. dromaea* are smaller species and that *P. groenlandica, P. tristis*, and *P. prosaica* cannot be differentiated from each other using this morphometric approach.

Table 2.—Examples of females of the *Pardosa groenlandica* species complex incorrectly identified using median septa shape in the morphological review.

Species	Correct/incorrect
P. groenlandica	3/8
P. dromaea	4/7
P. tristis	8/10
P. prosaica	6/12

Examples of error	Identified as	Correct species	Median septa shape
UAM100040085	*P. groenlandica*	*P. tristis*	parallel urn shape
UAM100050737	*P. groenlandica*	*P. prosaica*	narrow urn shape
UAM100040090	*P. groenlandica*	*P. prosaica*	narrow urn shape
UAM100040091	*P. groenlandica*	*P. prosaica*	narrow urn shape
UAM100039493	*P. groenlandica*	*P. prosaica*	narrow urn shape
UAM100045725	*P. dromaea*	*P. groenlandica*	wide urn shape
UAM100039724	*P. dromaea*	*P. tristis*	swelled "A" shape
UAM100039724	*P. dromaea*	*P. tristis*	swelled "A" shape
Chu 5	*P. tristis*	*P. groenlandica*	long "A" shape
UAM100040064	*P. tristis*	*P. groenlandica*	long "A" shape
UAM100045604	*P. prosaica*	*P. groenlandica*	wide urn shape
Chu 4	*P. prosaica*	*P. groenlandica*	wide urn shape
UAM100045726	*P. prosaica*	*P. groenlandica*	wide urn shape
UAM100045706	*P. prosaica*	*P. groenlandica*	wide urn shape
Chu 10	*P. prosaica*	*P. groenlandica*	wide urn shape
UAM100045758	*P. prosaica*	*P. tristis*	"A" shape

DISCUSSION

This review of the *Pardosa groenlandica* species complex replicated and re-evaluated previous studies and results presented in previous taxonomic literature (Kronestedt 1975; Dondale & Redner 1990; Dondale 1999). Published species descriptions enabled reliable identifications of four species, *P. albomaculata, P. lowriei, P. bucklei* and *P. groenlandica,* with the latter as the senior synonym of *P. tristis, P. prosaica,* and *P. dromaea*. We conclude that the morphological variation present in the four species, *P. groenlandica, P. dromaea, P. tristis,* and *P. prosaica, sensu* Dondale (1999) is insufficient to warrant species designation as we were unable to reliably separate the four species. We found no clear morphological species boundaries in these species; rather, there are morphological geographic trends and large amounts of genitalic variation in presumably conspecific members collected syntopically (i.e., in the same place and time). The amount of variation recorded is consistent with other *Pardosa* studies in which high amounts of variation have been found in *Pardosa* species groups both among species and within populations (Holm 1939, 1967; Kronestedt 1975, 1986, 1988, 1993; Vogel 2004). We could not find any previously unused characters that might help to diagnose these four named species. These results do not rule out the presence of multiple species living in sympatry as mentioned by Dondale (1999), but they highlight the fact that if this is the case, we could find no consistent morphological way to separate them.

Dondale (1999) provided descriptions that could identify some individuals of a population. For example, some *P. prosaica* can be diagnosed by the urn-shaped MS and by the constriction on the embolus, some *P. tristis* by the inverted T-shaped MS, and some *P. groenlandica* by the bottle-shaped MS. Specimens identified as *P. dronaea* were significantly smaller and showed a significantly smaller epigynal *p/q* ratio;

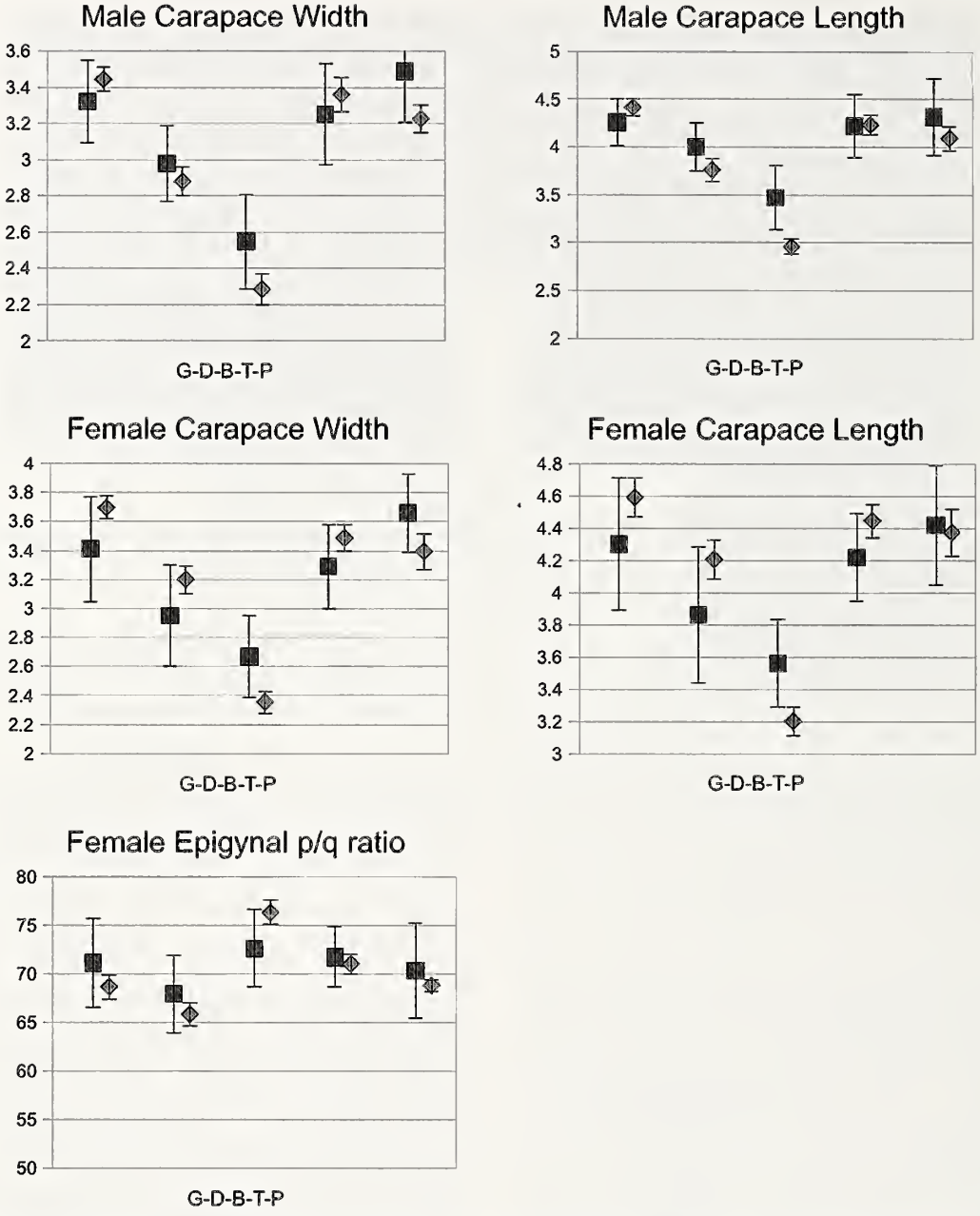

Figure 5.—Graphical comparison of morphometric characters used in Dondale (1999) with those collected in this study. Squares are Dondale's data; diamonds, results from this study. Error bars are one standard error. Y-axis is measured in mm, X-axis refers to order of species and corresponding column. G–*Pardosa groenlandica*; D–*P. dromaea*; B–*P. bucklei*; T–*P. tristis*; P–*P. prosaica*.

however, there are no male attributes for identification of these last three species. Additionally, the morphological differences that identify *P. dromaea* may be an artifact of the habitat, as the growth and development of juvenile *Pardosa* are affected by nutrition (Miyashita 1967; West-Eberhard 2005). The larger issue is that none of these identifiable forms exist in isolation from other variants showing a conglomeration of character states. It is as if the forms that had been described as species are just part of the variation. Thus identification of the variants requires the use of the proximity to specimens that are identified as one of the four identifiable forms. Use of this method for identification cannot be recommended because if species are sympatric there is no way of discerning species. Dondale (1999) and Vogel (2004) both present geographic regions for these species in which no sympatry is thought to occur (i.e., there should be only one species of the group present). This is a tricky assumption, which assumes sampling adequate to determine true species distributions, not just sampling occurrences. There is no doubt that both Dondale and Vogel felt that this assumption had been met, or else they likely would not have made such a statement; however, as our blind identification results show, either these regions contain multiple species or these species contain variation outside that described for them.

This difficulty in defining species boundaries is not unexpected, as lycosid spiders, and particularly *Pardosa*, show a great deal of conservation in some genital structures across genera, while also showing large amounts of genital variation in other structures among populations and species (Wallace

Table 3.—Measurements (in mm) of the *Pardosa groenlandica* species complex. Means significantly different from other species are identified by the first letter of the species name. Asterisk signifies measurements significantly different from Dondale (1999).

	Carapace width						Carapace length						Epigynum		
Species	Male	SE	sig.	Female	SE	sig.	Male	SE	sig.	Female	SE	sig.	Epigynal ratio	SE	sig.
P. groenlandica	3.44	0.066326549		3.69	0.08		4.42	0.08		4.59	0.12		68.64	1.27	
P. dromaea	2.88	0.08	gtpb	3.20	0.10	gtpb	3.76	0.12	gtpb	4.21	0.12		65.82	1.19	gdtp
P. bucklei	2.29	0.087037407	gdtp	2.35	0.08	gdtp	2.96	0.07	gdtp*	3.20	0.09	gdtp	76.29	1.25	gdtp
P. tristis	3.36	0.094657277		3.49	0.09		4.23	0.11		4.45	0.10		71.00	1.03	
P. prosaica	3.23	0.073514927		3.39	0.12		4.09	0.12		4.37	0.15		68.80	0.61	

1942; Dondale & Redner 1990). Additionally, spiders are thought to be prime candidates for evolutionarily fast reproductive morphological changes (Eberhard & Huber 2010). However, by replicating Dondale's (1999) previously used methods and by using a set of his voucher specimens, we confirmed that our sample of the *groenlandica* species group fell within the species demarcations of prior authors.

The morphological trends found in these data raise questions that morphology alone has been unable to answer. For example, the inverted T-shaped MS is only found in populations west of the Rocky Mountains. Other MS shapes are also found within these same populations. Therefore, it could be hypothesized that these are two or more species in sympatry, or that the inverted T-shaped MS is a historic geographic race that is experiencing some introgression from a more variable shaped MS race representing MS shapes other than the inverted T-shape. If the latter hypothesis is assumed, it questions gene flow due to these spiders' ability to disperse long distances when young via ballooning (Greenstone et al. 1987; Crawford et al. 1995), as no specimens with inverted T-shaped median septa were found north or east of the Rockies. These questions may yield to future analyses of molecular data.

CONCLUSION

Our evaluation of morphological identification characters for members of the *Pardosa groenlandica* species complex found them to be reliable for three species, *P. albomaculata, P. lowriei, P. bucklei.* We found no reliable morphological characters to separate the four species, *P. groenlandica, P. tristis, P. prosaica,* and *P. dromaea,* sensu Dondale (1999). Because these four species are sympatric with one or more of each other, and the published identification characters resulted in a 32% success rate we conclude that *P. tristis, P. prosaica,* and *P. dromaea* are junior synonyms of *P. groenlandica.* Using a blind identification analysis allowed us to remove the reliance of data types not directly associated with the specimen in hand. This type of test may be useful for taxonomists working with morphologically similar species to test identification characters independent of bias from other data sources.

TAXONOMY

Family Lycosidae Sundevall 1883

Pardosa C.L. Koch 1847

Pardosa groenlandica Thorell 1872

Lycosa groenlandica Thorell 1872:157; Jackson 1933:147, Pl. 1, Fig. 4; Holm 1939:77, Fig. 3. Lectotype male and paralectotype female from Disko Island, West Greenland (69°15′N, 3°32′W (Th. Fries). (Thorell Collection No. 244/1524a), 3 July 1871. Both deposited in the Swedish Museum of Natural History. Examined.

Lycosa iracunda Thorell 1877:514. Neotype male from Pikes Peak, 3660 m elevation, El Paso County, Colorado, 24 June 1940 (W.J. Gertsch and L. Hook), deposited in AMNH. Examined. Synonymized with *P. groenlandica* in Dondale 1999.

Lycosa indagatrix Thorell 1877:512. Holotype female from Denver (39°44′N, 104°59′W), Denver County, Colorado, 10 July 1875 (A.S. Packard, Jr.). Specimen lost or destroyed (Dondale 1999). Neotype male from South Platte River at 88th Street, Denver, Denver County, Colorado, 20 June 1985 (C.D. Dondale & J.H. Redner), deposited in CNC but unable to locate to examine. Synonymized with and designated type for *P. dromaea* in Dondale 1999.

Lycosa tristis Thorell 1877:510. Syntype female from "Idaho" (Idaho Springs, 39°44′N, 105°00′W), Clear Creek County, Colorado, 5 July 1875 (A.S. Packard, Jr.), and syntype female from Williams Canyon, "Manitou" (Manitou Springs, 38°51′N, 104°55′W), El Paso County, Colorado, 17 July 1875 (A.S. Packard, Jr.). Both lost or destroyed (Dondale 1999). Neotype female from Mt. Evans, 14,000 feet (4300 m) elevation (39°35′N, 105°38′W), Clear Creek County, Colorado, 25 July 1961 (B.H. Poole), deposited in CNC. Examined.

Lycosa dromaea Thorell 1878:395. New name for *L. indagatrix*, which was preoccupied.

Pardosa groenlandica Emerton 1894:423, Pl. 4, Fig. 1; Emerton 1902:79, Figs. 189, 190; Chamberlin 1908:200, Pl. 14, Fig. 6; Gertsch 1933:18; Comstock 1940:664, Fig. 731c; Braendegaard 1946:19, Figs. 6, 7; Levi 1951:225, Figs. 13, 14; Levi & Field 1954:456, Figs. 66, 68; Kronestedt 1975a:218, Figs. 3c, 4C–c; Dondale & Redner 1990:212, Figs. 300–304; Dondale 1999:439, Figs. 1, 14; Paquin & Dupérré 2003:163, Figs. 1807–1810; Vogel 2004:89, Figs. 71, 92.

Pardosa tristis Chamberlin & Ivie 1941:10; Roewer 1955:195; Dondale 1999:445, Figs. 2, 7, 8; Vogel 2004:91, f. 65, 91. New synonymy.

Pardosa nebraska Chamberlin & Ivie 1942:30, Pl. 7, Figs. 69, 70. Holotype male from 6 km west of Lexington (40°85′09″N, 99°85′59″W), Dawson County, Nebraska, 6 June 1933 (W. Ivie), deposited in AMNH. Examined. Synonymized with *P. dromaea* in Dondale and Redner 1990.

Pardosa prosaica Chamberlin & Ivie, 1947:21, Pl. 10, Figs. 89; Dondale 1999:446, Figs. 5, 10–13, 15. Holotype female from Quartz Creek, 15–16 miles (~ 24 km) N of Haycock

(65 13′N, 161 10′W), Seward Peninsula, Alaska, 11 August 1946 (R.D. Hamilton), deposited in AMNH. Not examined. New synonymy.

Pardosa dromaea Dondale & Redner 1990:209, Figs. 305–307; Dondale 1999:443, Figs. 4, 6; Vogel 2004:88, Figs. 72, 93. New synonymy.

Diagnosis.—*Pardosa groenlandica* is a member of the *modica* group (Kronestedt 1981); the species can be separated from all other members of the group by the males having a basally tapered embolus and a broad, flat, strongly curved conductor. Females have narrow, transverse atrial sclerites located along the posterior edge of the atrium, a median septum, which lacks elongated lateral protrusions from the anterior half of its length, and the median septum extends to the posterior edge.

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LITERATURE CITED

Crawford, R., P.M. Sugg & J.S. Edwards. 1995. Spider arrival and primary establishment on terrain depopulated by volcanic eruption at Mount St. Helens, Washington. American Midland Naturalist 133:60–75.

Dondale, C.D. 1999. Revision of the *groenlandica* subgroup of the genus *Pardosa* (Araneae, Lycosidae). Journal of Arachnology 27:435–448.

Dondale, C.D. & J.H. Redner. 1990. The insects and arachnids of Canada, Part 17. The wolf spiders, nurseryweb spiders, and lynx spiders of Canada and Alaska, Araneae: Lycosidae, Pisauridae, and Oxyopidae. Research Branch, Agriculture Canada, Publication 1856:1–383.

Eberhard, W.G. & B.A. Huber. 2010. Spider genitalia: precise maneuvers with a numb structure in a complex lock. Pp. 249–284. *In* The Evolution of Primary Sexual Characters in Animals. (J.L. Leonard & A. Córdoba-Aguilar, eds.). Oxford University Press, Oxford, U.K.

Emerton, J.H. 1894. Canadian Spiders. Transactions of the Connecticut Academy of Arts and Science 9:400–429.

Greenstone, M.H., C.E. Morgan & A. Hultsch. 1987. Ballooning spiders in Missouri, USA, and New South Wales, Australia: family and mass distributions. Journal of Arachnology 15:163–170.

Holm, Å. 1939. Araneae. *In* Insecta and Araneae collected in the Kangerdlugsuak Region of East Greenland by the British Expedition, 1935–36. (G.D. Hale Carpenter & ÅHolm, eds.). Annals and Magazine of Natural History (11) 3:72–80.

Holm, Å. 1967. Spiders (Araneae) from west Greenland. Meddelelser Grønland om Gronland 184:1–99.

Kronestedt, T. 1975. Studies on species of Holarctic *Pardosa* groups (Araneae, Lycosidae). I. Redescriptions of *Pardosa alboniaculata* Emerton and description of two new species from North America, with comments on some taxonomic characters. Zoologica Scripta 4:217–228.

Kronestedt, T. 1981. Studies on species of Holarctic *Pardosa* groups (Araneae, Lycosidae). II. Redescriptions of *Pardosa modica* (Blackwall), *Pardosa labradorensis* (Thorell), and *Pardosa sinistra* (Thorell). Bulletin of the American Museum of Natural History 170:111–124.

Kronestedt, T. 1986. Studies on species of Holarctic *Pardosa* groups (Araneae, Lycosidae). III. Redescriptions of *Pardosa algens* (Kulczyn'ski), *P. septentrionalis* (Westring), and *P. sodalis* Holm. Entomologica Scandanavia 17:215–234.

Kronestedt, T. 1988. Studies on species of Holarctic *Pardosa* groups (Araneae, Lycosidae). IV. Redescription of *Pardosa tetonensis* Gertsch and descriptions of two new species from the western United States. Entomologica Scandanavia 18:409–424.

Kronestedt, T. 1993. Studies on species of Holarctic *Pardosa* groups (Araneae, Lycosidae). V. Redescription of *Pardosa wasatchensis* Gertsch and description of a new species from Utah. Journal of Arachnology 21:175–183.

Miyashita, K. 1968. Growth and development of *Lycosa T-insignita* Boes. et. Str. (Araneae: Lycosidae) under different feeding conditions. Applied Entomological Zoology 3:81–88.

Packer, L., J. Gibbs, C. Shefield & R. Hanner. 2009. DNA barcoding and the mediocrity of morphology. Molecular Ecology Resources 9:42–50.

Platnick, N. 2013. The World Spider Catalog, Version 15.5. American Museum of Natural History, New York. Online at http://research.amnh.org/entomology/spiders/catalog/index.html (accessed 15 January 2013)

Roewer, C.F. 1955. Katalog der Araneae ven 1758 bis 1940, bwz. 1954. Bruzelles 2:1–1751.

Vogel, B.R. 2004. A review of the spider genera *Pardosa* and *Acantholycosa* (Araneae, Lycosidae) in the 48 contiguous United States. Journal of Arachnology 32:55–108.

Wallace, H.K. 1942. A revision of the burrowing spiders of the genus *Geolycosa*. Ameriean Midland Naturalist 27:1–62.

West-Eberhard, M.J. 2005. Developmental plasticity and the origin of species differences. Proceedings of the National Academy of Sciences 102:6543–6549.

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2013. The Journal of Arachnology 41:335–341

New records of Pennsylvanian trigonotarbid arachnids from West Bohemia, Czech Republic

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Abstract. New records of the extinct arachnid order Trigonotarbida are described from Upper Pennsylvanian (Moscovian: Bolsovian [=Westphalian C]) spoil heaps associated with the Týnec mine near the village of Týnec in West Bohemia, Czech Republic. Three specimens are recorded, two of which are incomplete opisthosomas assigned to Trigonotarbida *incertae sedis*. A third fossil is more complete and is described here as *Tynecotarbus tichaveki* gen. et sp. nov. Its familial position is uncertain, but the presence of a weakly lobed carapace and finely tuberculate body ornament suggests affinities with the 'eophrynid assemblage' *sensu* Dunlop & Brauckmann (2006) and particularly the family Lissomartidae from Mazon Creek, USA. In order to be comprehensive in our study, we include a complete list of Czech trigonotarbids.

Keywords: Fossil, Týnec, stratigraphy, new genus and species

Trigonotarbids are an extinct order of arachnids that ranged from the Upper Silurian (Přídolí) (Jeram at al. 1990) to the Lower Permian (Sakmarian) (Dunlop & Rössler 2013). Sixty-five valid species are currently recorded in the literature (Dunlop et al. 2013), and they occur most frequently in Pennsylvanian sediments in Europe and North America. Here they seem to represent one of the more common and abundant arachnid groups in Coal Measures ecosystems, their fossils regularly turning up at appropriate localities. Trigonotarbids are placed in the arachnid taxon Pantetrapulmonata Shultz 2007 [see also Shear et al. (1987) for details of synapomorphies] as the sister-group of the orders Araneae (spiders), Amblypygi (whip spiders), Thelyphonida (whip scorpions) and Schizomida (schizomids). They also share characters with the rare order Ricinulei (ricinluleids), which has led to speculation that ricinuleids may also be part of this wider pantetrapulmonate assemblage (see Dunlop et al. 2009). Trigonotarbid fossils are characterized by a segmented opisthosoma with eight or nine dorsally visible tergites, most of which are divided longitudinally into median and lateral plates. These animals evidently had mouthparts modified for biting (e.g., Shear et al. 1987) and are generally regarded as probably having been cursorial predators in Paleozoic terrestrial ecosystems (see overview in Garwood & Dunlop 2010).

Most of the Pennsylvanian trigonotarbids have been found at classic Westphalian localities associated with coal mining districts, such as the Saar and Ruhr areas of Germany (Guthörl 1934; Jux 1982), Silesia in Poland (Karsch 1882), former collieries or clay pits such as Coseley in the English West Midlands associated with the British Middle Coal Measures (Pocock 1911; Petrunkevitch 1949) and Mazon Creek in the USA (Petrunkevitch 1913). Trigonotarbids are also well represented in the Coal Measures of central and western Bohemia in the Czech Republic. Fifteen currently valid species have been described so far from this area (Table 1), although these are largely based on compression fossils that are prone to post-mortem alteration; e.g., shearing, stretching, truncation of body parts, etc. A number of these taxa are currently defined on rather trivial characters, relating to features such as ratios of body proportions, and we expect that some of the named species will eventually prove to be synonyms. Historical descriptions of Bohemian trigonotarbids can be found in Stur (1877), Kušta (1883, 1884), Frič (1901, 1904), Petrunkevitch (1953) and Přibyl (1958), with more recent summaries in Opluštil (1985, 1986:fig. 1) and a revision of three genera by Dunlop (1995a).

Here, we describe three Pennsylvanian trigonotarbids from a new Bohemian locality; namely spoil heaps near the village of Týnec. Two of these records are incomplete and are treated as Trigonotarbida *incertae sedis*. A third fossil is much better preserved and appears to represent a new genus and species, which we describe in detail below.

METHODS

The three specimens were obtained from the private collection of Mr. František Tichávek and have subsequently been deposited in the West Bohemian Museum, Pilsen. All are preserved as compression fossils in a gray–brown mudstone. We whitened the fossils with ammonium chloride and studied them under incident light using a binocular microscope. Photographs were made using an Olympus E410 camera. Immersion in 70% alcohol also improved the detection of morphological details, particularly cuticle. We studied the holotype of the new species under scanning electron microscopy (SEM) using a JEOL JSM-6380LV at the Institute of Geology and Palaeontology, Charles University, Prague. All measurements are in millimeters.

Locality and geological setting.—All three specimens described here were found among spoil deposits of the Týnec (formerly Masaryk or Austria 2) mine near the village of Týnec in West Bohemia, Czech Republic. In this mine, bituminous coal of Pennsylvanian (Moscovian) age was extracted between 1899 and 1965 from coal seams of the Radnice (Bolsovian substage) and Nýřany (Asturian substage) groups of the Kladno Formation; the former group being more important (Havlena 1964; Pešek 1996). This spoil heap was recently under threat of displacement due to intensive fire clay extraction and subsequent reclamation. During this process (between 2008 and 2010), a rich Pennsylvanian flora was collected in dark gray mudstones and examined in detail

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Table 1.—Trigonotarbids from the Czech Republic; arranged stratigraphically from youngest (above) to oldest (below). Data based on Opluštil (1985, 1986), Dunlop et al. (2013), Dunlop & Rössler (2013) and the primary literature, updated to reflect recent changes in nomenclature (cf. Dunlop 1995a; Harvey & Selden 1995; Garwood & Dunlop 2011). Only valid species listed; see Dunlop et al. (2013) for synonyms. Abbreviations: ISB – Intra Sudetic Basin, PB – Pilsen Basin, KRB – Kladno–Rakovník Basin, USB – Upper Silesian Basin.

Species	Locality	Age	Ma
Anthracomartus radvanicensis (Opluštil 1985)	Radvanice, ISB	Gzhelian	299–304
Anthracomartus bohemicus (Frič 1901)	Nýřany, PB	Moscovian [Asturian]	311–315
Anthracomartus carcinoides (Frič 1901)	Nýřany, PB	Moscovian [Asturian]	311–315
Anthracomartus elegans Frič 1901	Nýřany, PB	Moscovian [Asturian]	311–315
Anthracomartus nyranensis (Petrunkevitch 1953)	Nýřany, PB	Moscovian [Asturian]	311–315
Nyranytarbus hofmanni (Frič 1901)	Nýřany, PB	Moscovian [Asturian]	311–315
Nyranytarbus longipes (Frič 1901)	Nýřany, PB	Moscovian [Asturian]	311–315
Tyuecotarbus tichaveki gen. et sp. nov.	Týnec, PB	Moscovian [Bolsovian]	309–310
Aphantomartus areolatus Pocock 1911 (in Opluštil 1985)	Libušín near Kladno, KRB	Moscovian [Bolsovian]	309–310
Aphantomartus pustulatus Scudder 1884 (in Rössler 1998)	Libušín near Kladno, KRB	Moscovian [Bolsovian]	309–310
Trigonomartus spp. (in Opluštil 1985)	Libušín near Kladno, KRB	Moscovian [Bolsovian]	309–310
Aphantomartidae gen et sp. Indet. (in Opluštil 1985)	Mine Pokrok near Radnice, KRB	Moscovian [Bolsovian]	309–310
Anthracosironidae gen. et sp. Indet. (in Opluštil 1985)	Mine Gottwald-III, Kladno, KRB	Moscovian [Bolsovian]	309–310
Anthracomartus jmae (Opluštil 1986)	Vinařice near Kladno, KRB	Moscovian [Bolsovian]	309–310
Anthracomartus kustae Petrunkevitch 1953	Rakovník, KRB	Moscovian [Bolsovian]	309–310
Anthracomartus minor Kušta 1884	Rakovník, KRB	Moscovian [Bolsovian]	309–310
Planomartus krejcii (Kušta 1883)	Rakovník, KRB	Moscovian [Bolsovian]	309–310
Petrovicia proditoria Frič 1904	Petrovice near Rakovník, KRB	Moscovian [Bolsovian]	309–310
Stenotrogulus salmii (Stur 1877)	Ostrava-Karviná, USB	Serpukhovian	323–331

in order to gather data about the diversity of plant species in the Kladno Formation. During the course of these paleofloral investigations, a total of 32 species of fossil plant were found together with rare Pennsylvanian faunal elements (Tichávek & Bureš 2010), including the lophophorate *Microconchus*—originally thought to be the worm *Spirorbis*, but see Taylor & Vinn (2006) for a reinterpretation of pre-Mesozoic records—and the trigonotarbid arachnids. Although no stratigraphically indicative plant remains are associated with the arachnid specimens, the character of mudstone resembles that from the roof of the Upper Radnice Coal. This would render it Bolsovian in age (ca. 309–310 Ma), equivalent to the Westphalian C of Western European stage terminologies. The following Asturian substage is thus equivalent to the Westphalian D.

SYSTEMATIC PALEONTOLOGY

Order Trigonotarbida Petrunkevitch 1949

Remarks.—Petrunkevitch (1949) divided Karsch's (1882) original order Anthracomarti into two orders: subsequently emended to Anthracomartida and Trigonotarbida. The features Petrunkevitch used to separate these taxa were challenged by Dunlop (1996), and both groups were reunited under the then more widespread and clearly defined name Trigonotarbida. For a complete synonymy list of trigonotarbid higher taxa and further discussion, see Garwood & Dunlop (2011).

Family uncertain

Genus ***Tyuecotarbus*** gen. nov.

Type species.—*Tyuecotarbus tichaveki* gen. et sp. nov.

Etymology.—From the type locality of Týnec in West Bohemia and the typical trigonotarbid suffix tarbus; derived from the Greek *tarbos*, meaning terror/alarm.

Diagnosis.—Trigonotarbids characterized by a kidney-shaped to subtriangular carapace bearing a raised, triangular median region that hosts both the median eyes anteriorly and a row of three tubercles more centrally; carapace also with faint lateral lobation. Opisthosoma oval, and entire dorsal body surface ornamented with fine, granular tuberculation.

Figures 1–2.—*Tynecotarbus tichaveki* gen. et sp. nov., a new genus and species belonging to the extinct arachnid order Trigonotarbida from the Pennsylvanian (Moscovian, Bolsovian substage) of Týnec in the Pilsen Basin of West Bohemia, Czech Republic. 1. Overview of the holotype, West Bohemian Museum Pilsen, No. M00758; 2. The same, detail of the carapace region showing the fine granular ornament of the cuticle – arrowed are the putative median eyes, three larger tubercles on the midline and the faint lateral divisions of the carapace. Scale bars = 5 mm (1) and 2 mm (2).

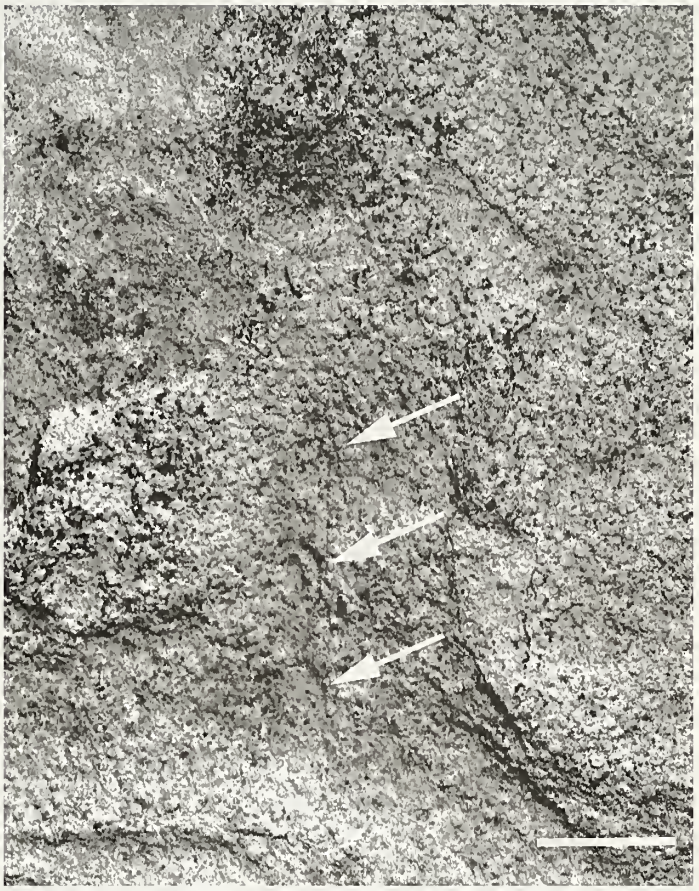


Figure 3.—*Tynecotarbus tichaveki* gen. et sp. nov. Holotype, scanning electron micrograph (SEM) of the central carapace region. Note again the granular cuticle ornament and the three larger, rounded tubercles towards the midline (arrowed). Scale bar = 1 mm.

Remarks.—Nine families of trigonotarbids are currently recognized, but there is no robust phylogenetic framework for their interrelationships. Our new Bohemian fossil does not fit comfortably into any of the accepted groupings. It was provisionally listed (and figured) as a member of the family Anthracosironidae by Tichávek & Bureš (2010). Based on its granular cuticle, it was also initially suspected to be an anthracomartid; see Garwood & Dunlop (2011) for a revision of Anthracomartidae. However, the absence of lateral eye tubercles on the carapace unequivocally excludes the families Anthracomartidae, Palaeocharinidae, Archaeomartidae (see especially Poschmann & Dunlop 2010:fig. 9), and probably the usually long-bodied Anthracosironidae, too. The remaining five trigonotarbid families are potentially a monophyletic group, united by this character of lateral eyes absent. Of these, Trigonotarbidae have a similarly raised median carapace region (cf. Pocock 1911; Petrunkevitch 1949), but their carapace is more obviously triangular and they lack both the granular body ornament seen in the new fossil and the faint lobes dividing the lateral carapace margins.

Three of the remaining four families also probably represent a monophylum, namely Aphantomartidae, Kreischeriidae and Eophrynidae. They were provisionally termed the 'eophrynid assemblage' by Dunlop & Brauckmann (2006) and can be characterized by the potential synapomorphies of an often

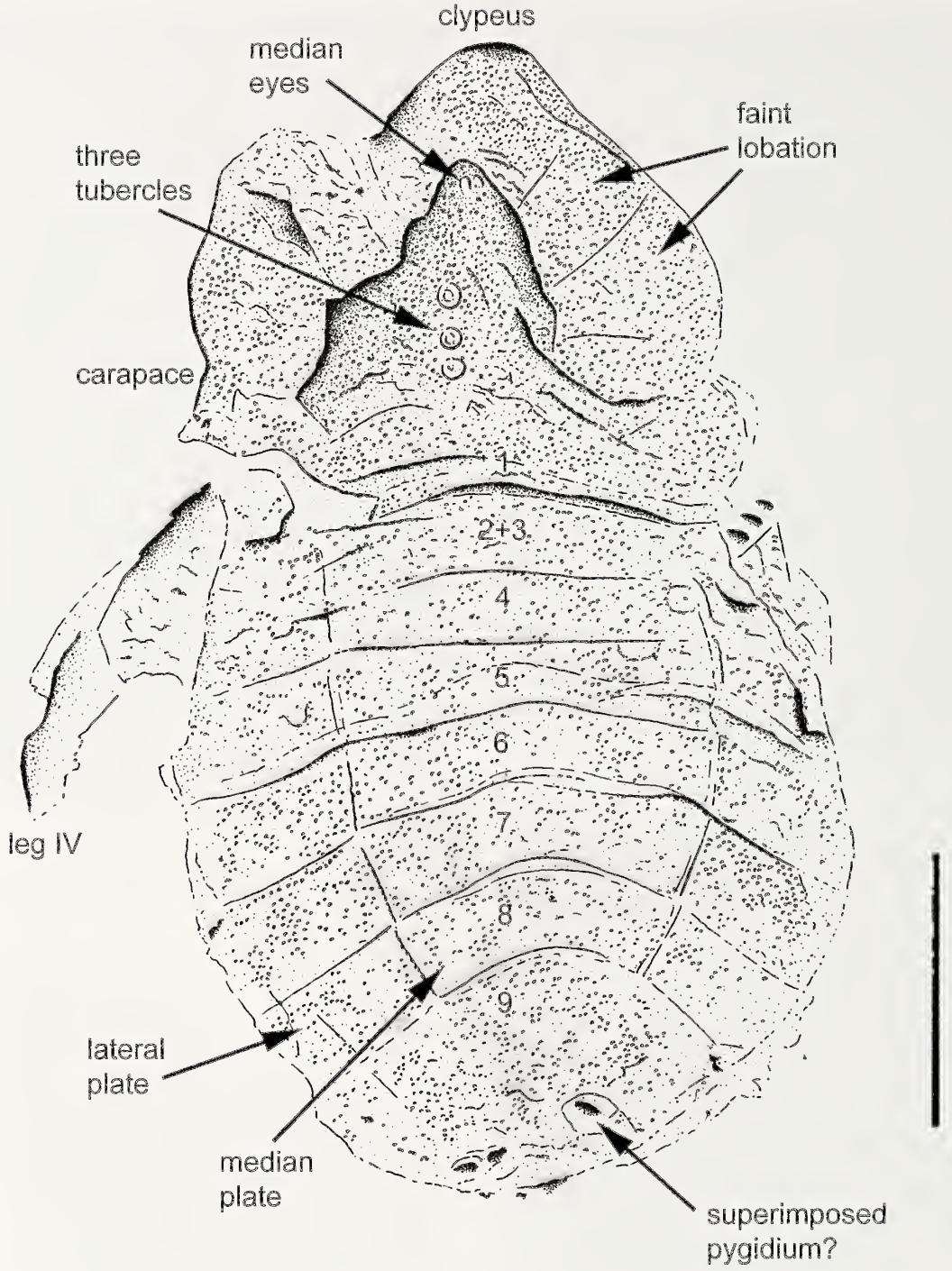


Figure 4.—Interpretative drawing of the holotype of *Tynecotarbus tichaveki* gen. et sp. nov.; opisthosomal segments numbered. Scale bar = 5 mm.

heavily ornamented dorsal body surface and deeply lobed carapace margins, typically with further lobation of the median carapace region as well; see, e.g., illustrations in Petrunkevitch (1953, Figs. 81, 82) and Dunlop (1995a). In this context, our new fossil—with only weak and barely discernible carapace lobation—cannot be accommodated into any of these 'eophrynid'-like families *sensu stricto*. In a wider context, there seem to have been transitional forms between the rather smooth and simply-constructed Trigonotarbidae and the larger and more robust and ornamented 'eophrynid'-like trigonotarbids.

Our new fossil preserves a unique combination of characters for trigonotarbids (see Diagnosis), which we believe justifies a new genus. We suspect that with its granular ornament and weakly lobed carapace, it falls phylogenetically somewhere into this transitional zone between Trigonotarbidae and the eophrynid assemblage. Two other genera appear to belong here, too. *Namaurotarbus* Poschmann & Dunlop 2010 (family uncertain) was raised for a trigonotarbid from Hagen Vorhalle in Germany, originally described by Dunlop & Brauckmann (2006: Figs. 1, 2). This rather squat German fossil has a more

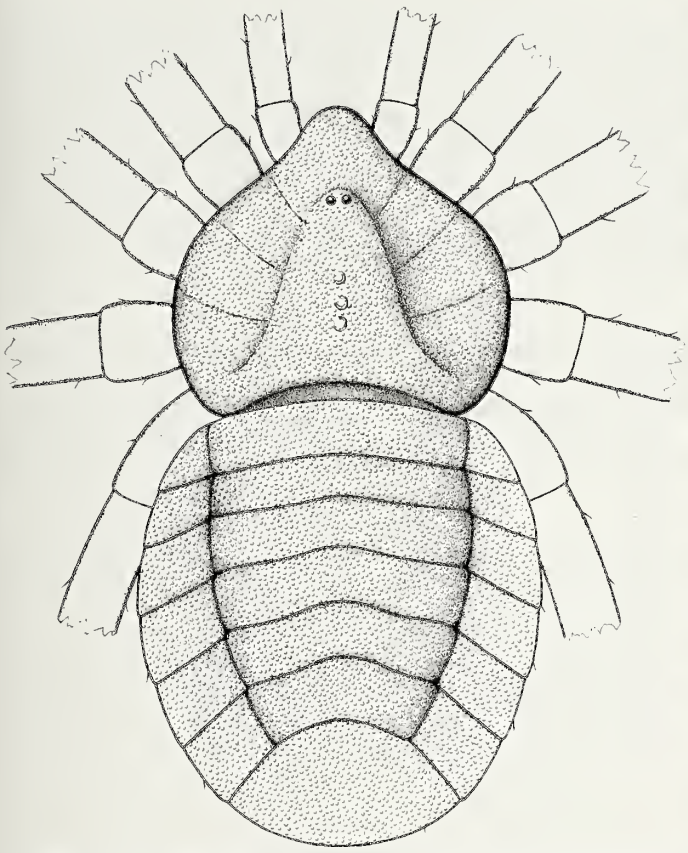
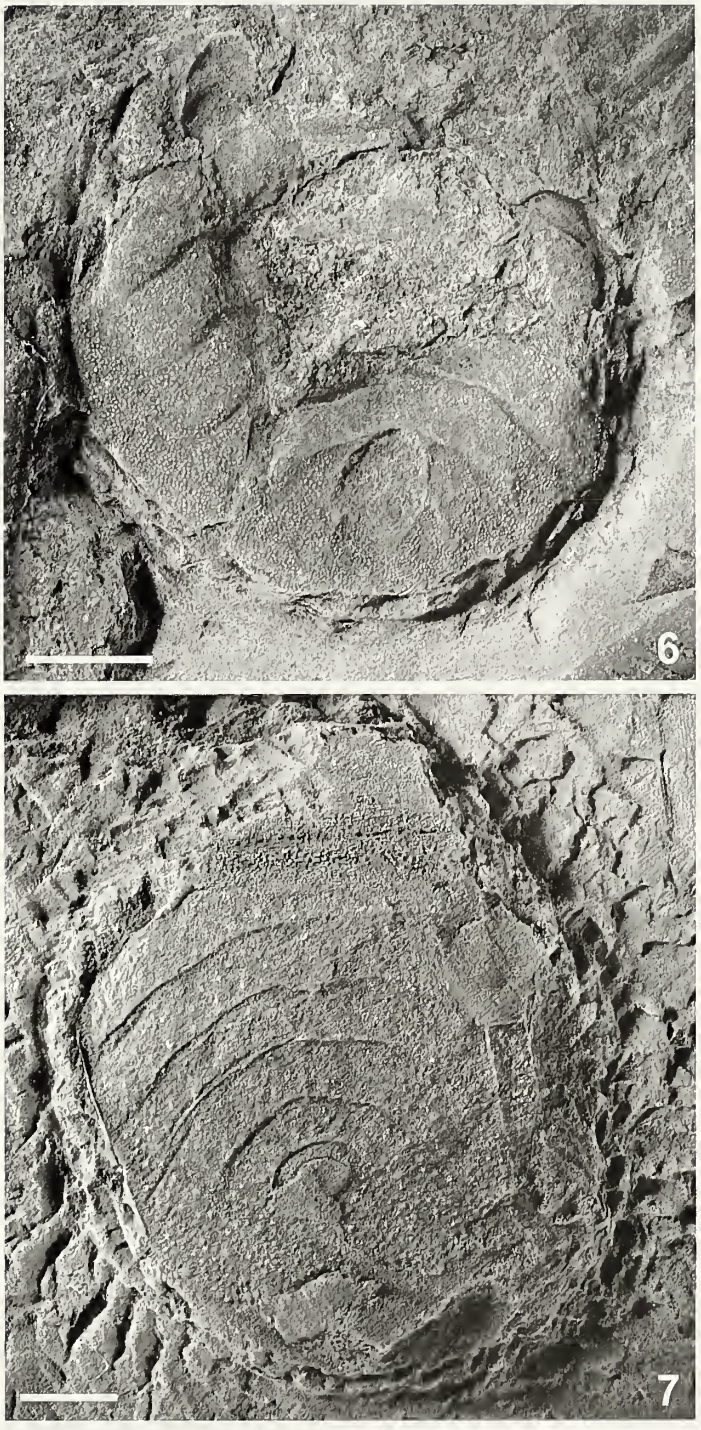


Figure 5.—Sketch reconstruction of the probable appearance of *Tynecotarbus tichaveki* gen. et sp. nov. in life; distal ends of pedipalps and legs equivocal in the original fossil and omitted here.



Figures 6–7.—Additional specimens assigned to Trigonotarbida *incertae sedis* held in the West Bohemian Museum Pilsen. 6. No M00759; 7. No M00760. Scale bars = 2 mm.

triangular carapace and quite strongly defined lateral carapace lobes. Unlike our new material, the median region of the carapace is also divided down the middle, and there is no granular cuticle ornament. We exclude our new fossil on these characters from *Namaurotarbus*.

A much better candidate is *Lissomartus* Petrunkevitch 1949 from Mazon Creek, USA. This genus was originally placed in Trigonotarbidae, but was raised to a new family, Lissomartidae, by Dunlop (1995b), who also redescribed its two constituent species. As in our new fossil, the carapace in *Lissomartus* is medially raised, has some larger tubercles behind the eyes toward the middle of the carapace, and there is weakly-defined lateral lobation of the carapace (Dunlop 1995b: Figs. 1–4, 7). However, *Lissomartus* differs from the new Bohemian arachnid in having a more triangular carapace profile, in lacking granular cuticle ornament, and in having the terminal (ninth) tergite divided into median and lateral plates. In the new fossil, tergite 9 is composed of a single plate only. On these characters, the new fossil does not fit clearly into Lissomartidae as it is currently defined, although we suspect this is where its affinities lie. Our concern would be that formally including it as a lissomartid cannot presently be justified by explicit apomorphies and may render the family paraphyletic with respect to more derived trigonotarbid taxa. Pending a detailed phylogenetic analysis, we prefer not to create another monotypic family group at this stage, and we suggest treating the new genus as being of uncertain family affinities. As noted above, with its weakly lobed carapace and light body ornament it seems to be part of a trigonotarbid lineage that was approaching the condition of the eophrynid assemblage.

Tynecotarbus tichaveki gen. et sp. nov.
(Figs. 1–5)

Trigonotarbida, Anthracosironidae: Tichávek & Bureš 2010:135–136, Figs. 6–7.

Material.—Holotype and only known specimen, No. M00758, Department of Palaeontology, West Bohemian Museum Pilsen, Czech Republic (ex private collection of F. Tichávek).

Type locality and horizon.—Týnec, West Bohemia, Czech Republic. Pilsen Basin, most probably the roof of the Upper Radnice Coal, Kladno Formation. Pennsylvanian, Moscovian, Bolsovian substage (= Westphalian C).

Diagnosis.—As for the genus.

Etymology.—In honor of Mr. František Tichávek, who discovered the holotype and kindly made it available for study.

Description.—Specimen in dorsal view (Figs. 1, 2) revealing carapace, opisthosoma and a partial leg. Cuticle of entire specimen with fine granular ornament (Fig. 3); average tubercle size ca. 0.1. Total body length 20.8. Carapace somewhat kidney-shaped to subtriangular, length 7.6, maximum width 8.7; slightly rounded anteriorly where it becomes drawn out into a short, blunt clypeus. Carapace slightly raised medially in a subtriangular central band; length 5.2; maximum width basally ca. 2.0. Median eyes faintly preserved toward the anterior tip of this band. No evidence of lateral eyes. Toward center of carapace three relatively large tubercles (diameter ca. 0.5) faintly preserved in a medial row (Figs. 2, 4). Margins of carapace weakly lobed; narrow demarcation lines (Figs. 2, 4) define three roughly subtriangular areas on each side of the raised median band. Single, incomplete and poorly preserved leg occurs on left side; total preserved length 6.0. Fairly slender; probably encompassing trochanter and femur of leg IV based on its posterior position, but individual limb articles barely distinguishable. Ventral features such as mouthparts and coxosternal region equivocal.

Opisthosoma broadly oval, slightly longer (13.2) than wide (max. ca. 12.0) and with smooth margins. Cuticle preserved as dark region centrally on the opisthosoma (better seen under alcohol immersion). Opisthosoma with nine dorsal tergites (Fig. 4); the first arched anteriorly into a so-called locking ridge, which would have tucked under the posterior margin of the carapace in life (Fig. 5). Visible length in fossil 1.3. Tergites in anterior part of opisthosoma slightly deformed, tergites 2–8 divided longitudinally into median and lateral plates; median plates quite wide and (from anterior to posterior) become increasingly longer and more procurved on their midlines. As in many trigonotarbids, tergites 2 and 3 are assumed to be fused into a single (macro)tergite. Circular feature visible toward back of the opisthosoma possibly the superimposed ventral pygidium (Fig. 4). Sternites and other ventral opisthosomal features equivocal. Opisthosoma lacks marginal spines or other ornament beyond the general granulation alluded to above.

Trigonotarbida *incertae sedis*
Figs. 6–7

Description.—No. M00759 (Fig. 6), Department of Palaeontology, West Bohemian Museum Pilsen; ventral opisthosoma only, almost circular in outline, length 8.0, maximum width 8.3. Seven sternites plus a circular pygidium (diameter 2) visible and cuticle with a granular ornament similar to that of No. M00758 (the holotype of *Tynecotarbus tichaveki* gen. et sp. nov.).

No. M00760 (Fig. 7), Department of Palaeontology, West Bohemian Museum Pilsen; ventral opisthosoma only, oval in outline, length 12.0, maximum width 11.0. Five sternites plus circular pygidium (diameter 1.5) visible and cuticle locally preserved. Sparse granulation, unlike No. M00758 (the holotype of *Tynecotarbus tichaveki* gen. et sp. nov.) and No. M00759, with tubercles of larger diameter (ca. 0.5).

Remarks.—The shape of the sternites and presence of a pygidium on the underside of the opisthosoma allow both of these fossils to be assigned with some confidence to Trigonotarbida. They are, however, too incomplete to place in any particular family or genus.

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LITERATURE CITED

Dunlop, J.A. 1995a. A redescription of two eophrynids (Arachnida: Trigonotarbida) from the Coal Measures (Carboniferous) of Ostrava, Czech Republic. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1995(8):449–461.

Dunlop, J.A. 1995b. Redescription of the Pennsylvanian trigonotarbid arachnid *Lissomartus* Petrunkevitch 1949 from Mazon Creek, Illinois. Journal of Arachnology 23:118–124.

Dunlop, J.A. 1996. Systematics of the fossil arachnids. Revue Suisse de Zoologie hors série: 173–184.

Dunlop, J.A. & C. Brauckmann. 2006. A new trigonotarbid arachnid from the Coal Measures of Hagen-Vorhalle, Germany. Fossil Record 9:130–136.

Dunlop, J.A. & R. Rössler. 2013. The youngest trigonotarbid *Permotarbus schuberti* n. gen., n. sp. from the Permian Petrified Forest of Chemnitz in Germany. Fossil Record 16:229–243.

Dunlop, J.A., C. Kamenz & G. Talarico. 2009. A fossil trigonotarbid with a ricinuleid-like pedipalpal claw. Zoomorphology 128:305–313.

Dunlop, J.A., D. Penney & D. Jekel. 2013. A summary list of fossil spiders and their relatives. *In* The world spider catalog, version 14.0. (N.I. Platnick, ed.). American Museum of Natural History, online at http://research.amnh.org/entomology/spiders/catalog/index.html

Frič, A. 1901. Fauna der Gaskohle und der Kalksteine der Permformation Böhmens. Vol. IV, part 2. Myriopoda pars II. Arachnoidea, pp. 56–63, pls. 153, 154, Prague.

Frič, A. 1904. Palaeozoische Arachniden. A Frič, Prague.

Garwood, R.J. & J.A. Dunlop. 2010. Fossils explained 58. Trigonotarbids. Geology Today 26:34–37.

Garwood, R.J. & J.A. Dunlop. 2011. Morphology and systematics of Anthracomartidae (Arachnida: Trigonotarbida). Palaeontology 54:154–161.

Guthörl, P. 1934. Die Arthropoden aus dem Carbon und Perms des Saar-Nahe-Pfalz-Gebietes. Abhandlungen der Preußischen Geologischen Landesanstalt (N.F.) 164:1–219.

Harvey, M.S. & P.A. Selden. 1995. *Nyranytarbus*, replacement name for *Hemiphrynus* Frič, 1901 (Trigonotarbida: Eophrynidae). Bulletin of the British Arachnological Society 10:74.

Havlena, V. 1964. [Geology of coal deposits 2.] Nakladatelství československé akademie věd. [In Czech]

Jeram, A.J., P.A. Selden & D. Edwards. 1990. Land animals in the Silurian: arachnids and myriapods from Shropshire, England. Science 250:658–661.

Jux, U. 1982. *Somaspidion hammapheron* n.gen. n.sp. – ein Arachnide aus dem Oberkarbon der subvaristischen Saumsenke NW Deutschlands. Paläontologische Zeitschrift 56:77–86.

Karsch, F. 1882. Ueber ein neues Spinnenthier aus der Schlesischen Steinkohle und die Arachnoiden überhaupt. Zeitschrift der Deutschen Geologischen Gesellschaft 34:556–561.

Kušta, J. 1883. *Anthracomartus krejcii*, eine neue Arachnide aus dem Böhmischen Karbon. Sitzungsberichte der Königlich Böhmischen Gesellschaft der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse 1883:7.

Kušta, J. 1884. Neue Arachniden aus der Steinkohlenformation von Rakonitz. Sitzungsberichte der Königlich Böhmischen Gesellschaft der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse 1884:398–401.

Opluštil, S. 1985. New findings of Arachnida from the Bohemian Upper Carboniferous. Věstník Ústředního ústavu Geologického 60:35–42.

Opluštil, S. 1986. *Promygale janae* sp. n., the new anthracomartid (Arachnida) from the Upper Carboniferous of central Bohemia. Věstník Ústředního ústavu Geologického 61:287–292.

Pešek, J. 1996. [Geology of the basins of the central Bohemian area]. Český geologický ústav. Prague. [In Czech]

Petrunkevitch, A.I. 1913. A monograph of the terrestrial Palaeozoic Arachnida of North America. Transactions of the Connecticut Academy of Arts and Sciences 18:1–137.

Petrunkevitch, A.I. 1949. A study of Palaeozoic Arachnida. Transactions of the Connecticut Academy of Arts and Sciences 37:69–315.

Petrunkevitch, A.I. 1953. Palaeozoic and Mesozoic Arachnida of Europe. Memoirs of the Geological Society of America 53:1–128.

Pocock, R.I. 1911. A monograph of the terrestrial Carboniferous Arachnida of Great Britain. Monographs of the Palaeontographical Society 64:1–84.

Poschmann, M. & J.A. Dunlop. 2010. Trigonotarbid arachnids from the Lower Devonian (Lower Emsian) of Alken an der Mosel (Rhineland-Palatinate, SW Germany). Paläontologische Zeitschrift 84:467–484.

Přibyl, A. 1958. Some new Carboniferous arachnids from the Ostrava-Karviná coal district. Časopis pro Mineralogii a Geologii 3:425–434.

Rössler, R. 1998. Arachniden-Neufunde im mitteleuropäischen Unterkarbon bis Perm – Beitrag zur Revision der Familie Aphantomartidae Petrunkevitch 1945 (Arachnida, Trigonotarbida). Paläontologische Zeitschrift 72:67–88.

Shear, W.A., P.A. Selden, W.D.I. Rolfe, P.M. Bonamo & J.D. Grierson. 1987. New terrestrial arachnids from the Devonian of Gilboa, New York. American Museum Novitates 2901:1–74.

Shultz, J.W. 2007. A phylogenetic analysis of the arachnid orders based on morphological characters. Zoological Journal of the Linnean Society 150:221–265.

Stur, D. 1877. Die Culm-Flora der Ostrauer und Waldenburger Schichten. Abhandlung der königliche geologische Reichanstalt 4:5.

Taylor, P.D. & O. Vinn. 2006. Convergent morphology in small spiral worm tubes ("*Spirorbis*") and its palaeoenvironmental implications. Journal of the Geological Society 163:225–228.

Tichávek, F. & J. Bureš. 2010. Carboniferous flora and rare fauna discoveries in the dump of the Austria mine 2 at Týnec (Czech Republic). Erica, Plzeň 17:131–140.

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Variation and possible function of egg sac coloration in spiders

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Abstract. Coloration of the egg sacs of spiders varies widely to the human eye, both across and within taxonomic groups. These differences in coloration are expected with differences in the biology and ecology of different species. Here we measure the spectral properties of the egg sacs of 15 species in six families. Ultraviolet chroma, red chroma, and particularly overall brightness vary widely across and within taxonomic groups. We discuss the spectral properties of the silk of the egg sacs in the context of the physical characteristics of the silk, the reflective properties of the background, the environmental illumination, and the natural history and behavior of the spider species. In most cases, the spectral characteristics of the egg sacs seem to reduce their conspicuousness against the background and in those cases in which the coloration does not reduce the contrast in relation to the background, the low environmental light available may help to camouflage the egg sacs.

Keywords: ancestral state, brightness, camouflage, conspicuousness, predator avoidance, red chroma, spectral properties, UV chroma

The different characteristics of egg sacs in spiders are thought to have evolved to protect the female's reproductive investment in several ways (Gertsch 1949). For instance, the multiple layers of silk of varying consistency in egg sacs create and maintain an appropriate internal environment for embryo development (Hieber 1985, 1992a), and they also serve as a barrier to prevent some parasites and predators from reaching the eggs and embryos (Austin 1985; Hieber 1992a,b). Other features, such as long egg sac pedicels and webs built exclusively to maintain the egg sac, further reduce access to the eggs by parasites and predators (Hieber 1992b).

Spider maternal behavior also aids in reducing parasitism and predation. For example, females of many species (e.g., *Tengella radiata* and theridiids) protect the egg sacs, especially during the first days after producing them (Bristowe 1958; Barrantes 2008), when eggs are likely more susceptible to parasitoids. Some spiders (e.g., lycosids and pisaurids), attach the egg sacs to their chelicerae or spinnerets until the spiderlings emerge (Foelix 2011). Other spiders camouflage the egg sacs with silk stabilimenta (Herberstein et al. 2000; Eberhard 2003), pieces of debris (Barrantes 2007), or wrap egg sacs in a leaf (Moya et al., 2010) to protect eggs against parasites and predators.

The coloration of egg sacs varies widely, but there is no information on the pigments responsible for the differences in color, or on their roles in camouflage. Effectiveness in camouflage depends on color, shape, and especially the contrast created by the external layer of the egg sac against the visual background (Craig 2003). The color of the egg sac may not affect protection of some spiders that produce and maintain their egg sacs deep inside burrows or silk tunnels. By contrast, in species that construct and maintain egg sacs in more exposed places, the coloration of the external layer may reduce conspicuousness and provide additional camouflage (e.g., many Theridiidae, Nielsen 1932). Two possible questions to address in relation to the spectral properties of the egg sacs are the following. 1) Does coloration of egg sacs relate to their level of exposure? 2) Is the eolor of the egg sac associated with the spider's taxonomic (phylogenetic) group?

With few exceptions, the web silk of most spiders is unpigmented (Craig et al. 1994; Craig 2003). *Nephila clavipes* is one of the few species that adds yellow pigment to its silk web (Craig et al. 1996), although the origin of this pigment is unknown. There is a subtle variation in the color of web silk among webs of *N. clavipes*, with more intense yellow correlating with greater light in the environment in which the spider constructs its web (Craig et al. 1996). On the other hand, the color of the silk used by spiders to construct the external layer of their egg sacs varies widely, at least to the human eye, among species within a given family and among families. In this study we objectively quantify the colors of the silk cocoon from 15 species of spiders in six families, and discuss their potential ecological roles.

METHODS

We photographed and measured the reflectance of field-collected egg sacs of 15 spider species (Table 1) deposited in the collection of the Museo de Zoología, Universidad de Costa Rica, San José, Costa Rica in 2012. We measured from one to five egg sacs per species according to their availability in the collection (Table 2). All egg sacs were collected after the spiderlings emerged, and were kept in dry vials in the dark until measurements were conducted.

We photographed the egg sacs using a Nikon Coolpix 4500 camera attached to a dissecting microscope in order to show the variation in coloration of the egg sacs as perceived by the human eye. We collected several images of each spider egg sac under different light conditions and then selected the image that best matched the color of the egg sac as perceived by two observers (G. Barrantes and C. Sánchez-Quirós) to display in Fig. 1.

To obtain silk reflectance measurements, we used an Ocean Optics USB 2000 spectrometer and a PX-2 flash light source (Ocean Optics, Dunedin, Florida) connected to a bifurcated probe (Ocean Optics R400-7-SR). Such a setup allowed us to obtain all measurements at normal incidence to the reflective surface. We kept the reflectance probe at a fixed distance of

Table 1.—Characteristics of the habitat and behavior of 15 Costa Rican spider species.

Family/Species	Egg sac background
Filistatidae	
Kukulcania hibernalis (Hentz 1842)	This synanthropic species constructs its web in dark places and retains the egg sacs within a dense tunnel retreat constructed of silk.
Oxyopidae	
Peucetia viridans (Hentz 1832)	Constructs its egg sacs under leaves of herbs and bushes between 0.5 to 1.7 m above the ground in very exposed locations of early secondary vegetation and forest edges.
Deinopidae	
Deinopis sp.	Constructs its egg sacs with a silk pedicel ca. 2 cm long, attached to twigs or vines, usually between 0.5 to 2 m above the ground in understory of mature, old secondary forests, and plantations.
Uloboridae	
Zosis geniculata (Olivier 1789)	Attaches the egg sacs to its web, which is constructed in dark locations near the forest floor or in buildings.
Theridiosomatidae	
Wendilgarda sp. Keyserling 1886	Constructs its egg sac attached by a silk pedicel of approximately 2 cm to leaves or twigs between 0.5 to 1.5 m above the ground, near streams in mature forests.
Theridiidae	
Latrodectus hesperus Chamberlin & Ivie 1935	Constructs its web under rocks or logs in open areas. The female retains the egg sacs in a silk tunnel.
L. geometricus C. L. Koch 1841	Egg sac constructed inside dense silk retreat deep inside web, usually outside buildings, less often inside.
L. mirabilis (Holmberg 1876)	Constructs its web between rocks (outcrop of large rocks) near the ground (5 to 10 cm above the ground), egg sac protected underneath rocks.
Steatoda grossa (C. L. Koch 1838)	Constructs its web under stones in dark places of rain forests and under furniture inside buildings, egg sac attached to the upper sheet in the web.
Anelosimus studiosus (Hentz 1850)	Builds its web in branches, twigs and leaves of bushes in open areas,egg sac constructed inside the silk tunnel retreat of the web.
A. pacificus Levi 1956	Builds its webs on leaves at tips of twigs of trees in open areas, egg sac built between two leaves.
Tidarren sisyphoides (Walckenaer 1841)	Builds its web on bushes in open areas, egg sac retained inside retreats constructed of plant debris, usually pieces of leaves. *T. sisyphoides* and *P. tesselata* construct their webs on bushes in open areas, while *P. tepidariorum* builds its web outside buildings.
Parasteatoda tesselata (Keyserling 1884)	Similar to *T. sisyphoides*.
P. tepidariorum (C. L. Koch 1841)	Usually builds its web outside buildings, egg sac often retained inside retreats constructed of plant debris.
Nesticodes rufipes (Lucas 1846)	This synantropic species constructs web in relatively dark sites and attaches its egg sac to silk threads at the top of its web, which it places inside buildings.

5 mm from the egg sacs during the measurements, using a rubber probe holder. This rubber holder also excluded the external light from the reflectance probe. For each egg sac, we measured the reflectance properties at five different haphazardly selected regions. Reflectance measurements were made relative to that of a diffuse pure white standard (WS-1 Ocean Optics). Our reflectance analyses were restricted to wavelengths from 300 to 700 nm, a range that includes ultraviolet (UV) through red colors.

Spectral curves for each egg sac were visually inspected by one of us who had not previously seen the egg sacs or images of them (P.-P. Bitton), and any measurement that deviated strongly from the others was removed from further analyses. We did this, for example, when one spectral curve was clearly different in shape or overall reflectance from the remaining four repeated measures. Differences in measurements most likely occurred when the probe was not placed directly against the surface of the egg sac when collecting data. We took the average of the remaining curves and measured color variables in the consolidated data set. For every egg sac measured, we determined 1) the brightness as the average reflectance over the 300–700nm range,

$$\sum_{\lambda 300}^{\lambda 700} R_i \Big/ n$$

where R_i is the percentage reflectance at the *ith* wavelength (λ_i) and n is the number of wavelength intervals), 2) the ultraviolet (UV) chroma,

$$\sum_{\lambda 300}^{\lambda 400} R_i \Big/ \sum_{\lambda 300}^{\lambda 700} R_i$$

and 3) the red chroma,

$$\sum_{\lambda 600}^{\lambda 700} R_i \Big/ \sum_{\lambda 300}^{\lambda 700} R_i$$

All measures are described in more detail in Montgomerie (2006). We elected to describe the spectral reflectance of the egg sacs with UV and red chroma because most of the variation among species occurred in these regions. We did not determine the hue for any of the egg sacs measured because all spectral curves peaked near 300nm or 700nm, rendering this common color descriptor uninformative. The spectral data were manipulated and analyzed using the R package "pavo"

Table 2.—Silk egg sac color characteristics for 15 species of Costa Rican spiders. Brightness is the average reflectance relative to a white standard (see methods) over the 300–700nm range. Ultraviolet (UV) chroma and red chroma are the contribution of the 300–400nm range and 600–700nm range, respectively, to the total brightness. Values represent means ± SD obtained from *n* samples.

Species	*n*	Brightness (%)	UV chroma (%)	Red chroma (%)
Filistatidae				
Kukulcania hibernalis	2	43.4 ± 9.1	24.2 ± 3.2	26.2 ± 2.4
Deinopidae				
Deinopis sp.	5	7.3 ± 0.3	44.3 ± 1.1	24.3 ± 1.7
Uloboridae				
Zosis geniculata	5	32.8 ± 6.5	17.0 ± 0.7	34.6 ± 0.9
Oxyopidae				
Peucetia viridans	1	10.8	29.7	31.6
Theridisomatidae				
Wendilgarda sp.	1	17.1	21.4	30.3
Theridiidae				
Latrodectus hesperus	1	12.4	13.9	32.4
L. geometricus	5	11.7 ± 3.3	14.8 ± 1.7	30.7 ± 1.8
L. mirabilis	2	28.5 ± 1.0	12.8 ± 1.5	27.9 ± 0.9
Steatoda grossa	4	13.3 ± 1.3	25.1 ± 1.6	21 ± 0.5
Anelosimus studiosus	1	16.3	25.2	24.8
A. pacificus	2	47.0 ± 12.7	17.1 ± 2.4	24.1 ± 1.8
Tidarren sisyphoides	5	5.2 ± 0.4	23.7 ± 1.8	35.4 ± 1.1
Parasteatoda tesselata	1	21.0	16.6	35.6
P. tepidariorum	5	10.5 ± 3.7	25.1 ± 4.3	33.3 ± 2.3
Nesticodes rufipes	5	10.0 ± 0.9	15.4 ± 0.5	34.3 ± 1.9

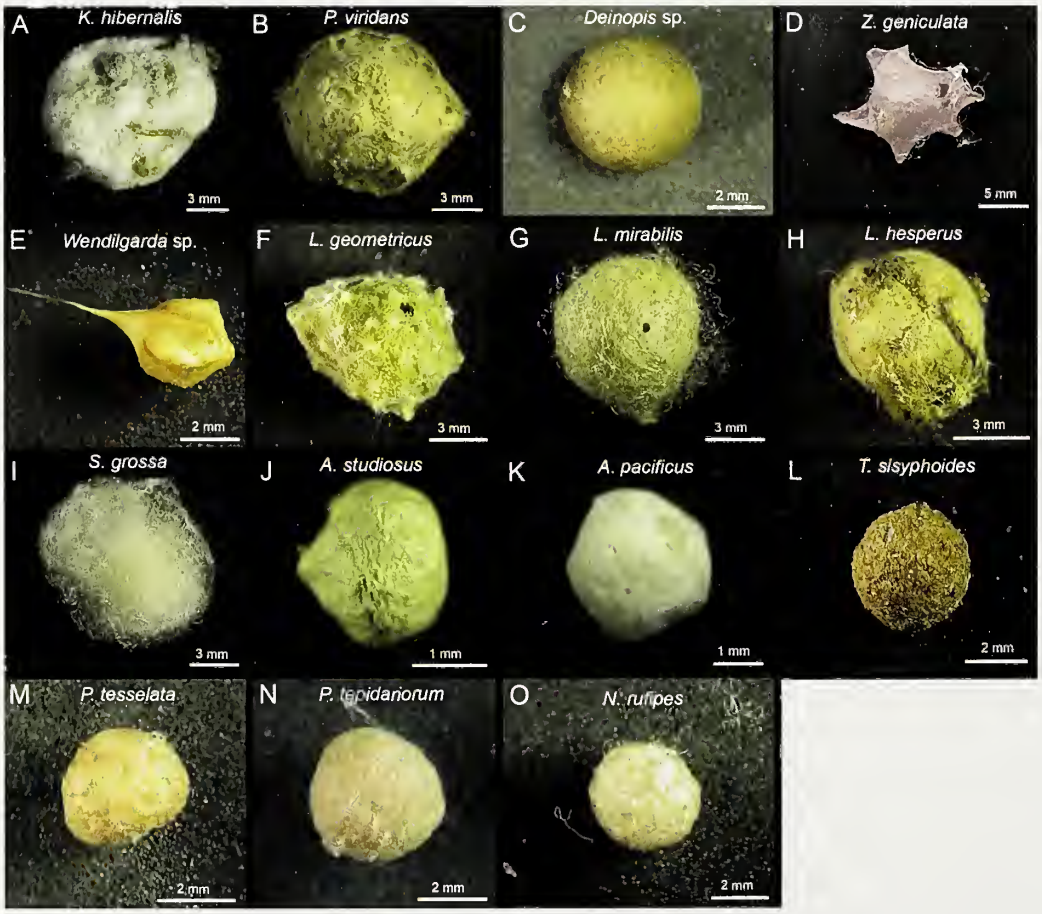

Figure 1.—Egg sacs of 15 species of Costa Rican spiders.

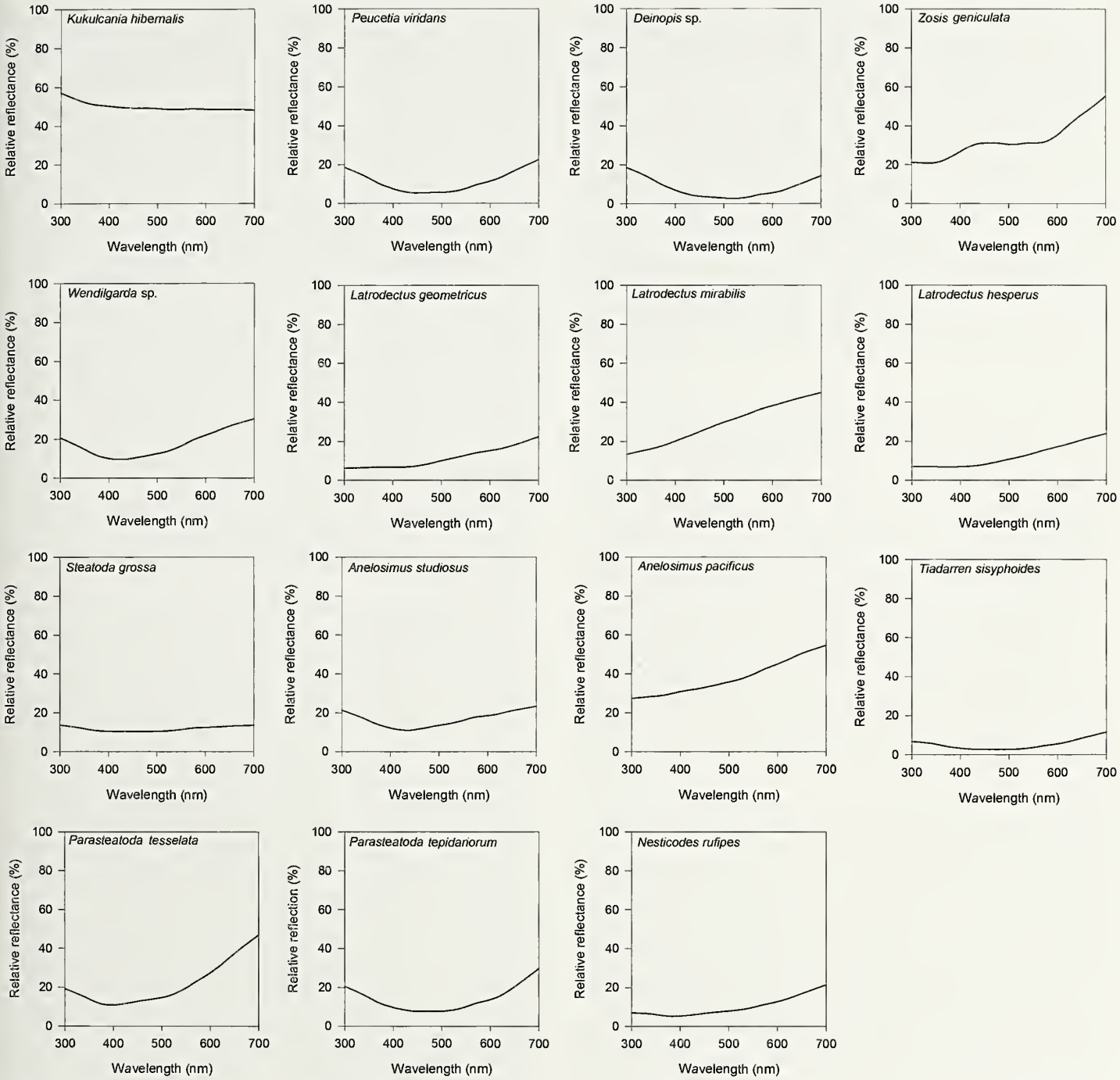

Figure 2.—Mean spectral curves of silk egg sacs for 15 species of Costa Rican spiders. Percentage reflectance is relative to a pure diffuse white standard (see methods).

(Maia et al. 2013). Authorities for the scientific names of all 15 species in this study are listed in Table 1.

RESULTS

The silks of the spider egg sacs differed extensively in their brightness [(mean = 19.1% ± SD = 13.0%), UV chroma (21.8% ± 8.1%) and red chroma (29.7% ± 4.7%); Table 2]. Within the human visible spectrum, the color of the egg sacs ranged from almost black (*Tidarren sisyphoides*: brightness = 5.2%), to pale gray (*Kukulcania hibernalis*: brightness = 43.4%), with most egg sacs appearing brown (Fig. 1). In 10 of the 15 species, brightness (%) increased with wavelength (nm) (e.g., *Latrodectus* spp.: Fig. 2). Several of the egg sacs that appear brown to the human eye had relatively high UV chroma (e.g., *Peucetia viridans* and *Deinopis* sp.); species that are sensitive to UV wavelengths would likely be able to distinguish between brown egg sacs with low and high UV chroma. In *Deinopis* sp., the UV wavelengths contributed a very large portion of the overall brightness (UV chroma = 44.3%) and would appear more "UV" than red to UV-

sensitive species (red chroma = 24.3%). In contrast, silk of the egg sacs of the Uloboridae (e.g., *Zosis geniculate*), the sister family of Deinopidae, had a low UV reflectance, but high reflectance toward the red (Fig. 2).

Within the Theridiidae, silk spectral properties were generally the same across the three *Latrodectus* species, the two *Parasteatoda* species and *Nesticodes rufipes* (Table 2). The brightness of *Steatoda grossa* was similar to the previous species but with a relatively high UV chroma, while *Tidarren sisyphoides* had a very low brightness (brightness = 5.2%) and a very high value of red chroma (35.4%). The two species of *Anelosimus* were very different from each other (Fig. 2). *Anelosimus studiosus* was relatively dark (brightness = 16.3%) and had very high UV chroma (25.2%), while *A. pacificus* was much brighter (brightness = 47%) with a relatively low UV chroma (17.1%).

DISCUSSION

In this first study of the spectral characteristics of egg sac silk, we show extensive variation among species in their brightness and chroma. Of particular interest, much variation was found in reflectance in the UV range, a characteristic that is not detectable by the human eye. The silk of the egg sacs of many spiders had a high reflectance toward the red range, giving them a brownish appearance, a feature that probably evolved to reduce the conspicuousness of the egg sacs. Conspicuousness could be reduced if the colored silk of egg sacs reflects wavelengths similar to those reflected by the background, as apparently occurs with the pigmented silk of *Neplila clavipes* webs (Craig et al. 1996). In addition, the low intensity of light in some environments (Endler 1993) allows red-brownish egg sacs to blend with the surroundings more readily than uncolored egg sacs. Both of these hypotheses remain to be tested.

High reflectance in the silk of webs in the UV range is apparently an ancestral characteristic of spiders (Craig et al. 1994; Bond & Opell 1999). Silk of webs in the suborder Mygalomorphae, as well as the sticky cribellate silk of basal Araneomorphae and Deinopoidea (Deinopidae and Uloboridae) have high UV reflectance, while the sticky silk of Araneoidea species have a flat or low UV reflectance (Craig et al. 1994). These differences in UV reflectance have been correlated with the ambient light conditions where spiders of these groups build their webs (Bond & Opell 1999; Craig 2003). Spiders whose silk web has high UV reflectance construct their webs in dim environments (Craig et al. 1994; Bond & Opell 1999; Craig 2003), while webs with low UV reflectance constructed in light environments are a shared derived character for Araneoidea (Bond & Opell 1999). However, many species in Araneoidea also build webs in dark environments (e.g., *Nesticus* in Gertsch 1949 and *Spilasma* GB unpublished data) and the silk reflectance properties of these species remains unexplored.

The UV reflectance of egg sacs does not always match that of the silk webs of the same spider groups. For instance, UV reflectance is high in the silk web and egg sacs of *Kukulcania hibernalis* (Filistatidae) and *Deinopis* sp. (Deinopidae) (Craig et al. 1994; Bond & Opell 1999), and in the egg sacs of *Peucetia viridans* (Oxiopidae). However, in contrast to the silk web of uloborids (Craig et al. 1994), the UV reflectance in the silk of egg sacs of *Zosis geniculata* (Uloboridae) is low. In addition to high UV reflectance in the silk of egg sacs of *P. viridans* and *Deinopis*, their silk also has a high reflectance toward the red, similar to the egg sacs of *Z. geniculata*. The UV reflectance in the silk of egg sacs of these species may be an ancestral trait, similar to the high UV reflectance in their silk web (Bond & Opell 1999; Craig 2003), although to examine the evolution of reflectance on the silk of the outer wall of egg sacs would only be possible with more extensive and comparable data (aciniform silk). Yet the high red reflectance of egg sacs has presumably evolved within these families to reduce the visual contrast of the egg sacs against the background, as they appear to blend with surrounding structures of similar coloration. For instance, *P. viridans* maintain their egg sacs under leaves of grasses and bushes in forest edges and patches of secondary vegetation where dead leaves with similar color to the egg sacs (Fig. 1B) are abundant (G. Barrantes unpublished data). *Deinopis* sp. live in dim habitats, and their egg sacs hang near dead twigs and vines that to the human eye match the coloration of their egg sacs. Similarly, Uloboridae (e.g., *Z. geniculata*) inhabit dim sites (Craig et al. 1994; Bond & Opell 1999) and the color of their egg sacs vary from yellow to red-yellow to brown, to purple, to grayish (Opell 1989, GB unpublished data), probably reducing visual contrast with the background.

We included two families in the clade Araneoidea in this study: Theridiosomatidae (*Wendilgarda* sp.) and Theridiidae (10 species). The reflectance of the silk of the egg sacs of *Wendilgarda* is relatively high in the UV and red, similar to that of *Deinopis* and *P. viridans*. All theridiosomatids inhabit dense forests. They construct their webs and, in most species, also their egg sacs near the forest floor (Coddington 1986), the darkest stratum in the forest. There are some exceptions; for instance, *Wendilgarda* construct their webs above the surface of streams, and their egg sacs are hung near the end of twigs and leaves of bushes at about 1 m above the ground and near streams (Coddington 1986; Eberhard 2001; G. Barrantes unpublished data). Thus the light-brown egg sacs of *Wendilgarda* are in brighter environments and may be more exposed than those of other genera of Theridiosomatidae, which retain the egg sacs on the web, or hang them on the dense vegetation of understory forests (Coddington 1986). The coloration of the egg sacs of *Wendilgarda* possibly reduces their conspicuousness, since plant debris (dead leaves and twigs) with similar coloration hangs abundantly on understory plants.

Within the family Theridiidae, the spectral properties of egg sac silk vary widely across species. The pattern of reflectance of the three *Latrodectus* species is very similar, particularly *L. geometricus* and *L. hesperus*. In all three species the silk of egg sacs has a high reflectance toward the red. However, the reflectance of the silk of the egg sacs of *S. grossa*, the sister genus of *Latrodectus* (Agnarsson 2004), is not saturated in any of its range, appearing to the human eye as white (Figs. 1 & 2). *Steatoda grossa* construct their webs under stones in rain forests (Levi 1962) or in dark locations inside buildings (Aisenberg et al. 2011), while all *Latrodectus* species construct their webs and egg sacs in protected but bright environments (though *L. geometricus* often build their webs and egg sacs inside buildings). The spectral properties of the egg sacs of the two species of the genus *Anelosimus* (*A. studiosus* and *A.*

pacificus) differ markedly. The silk of the egg sac of *A. studiosus*, which is retained inside the silk tunnel web, is relatively dark with similar UV and red reflectance, while egg sacs of *A. pacificus*, in which the adult female positions the egg sac between two live leaves (Agnarsson et al. 2006), are brighter and have high red reflectance. The other theridiids inhabit bright environments and retain their egg sacs, the silk of which has relatively high red reflectance, within retreats constructed with plant debris (e.g., pieees of dead leaves: Triana et al. 2012). Retaining brown-reddish egg sacs inside close retreats constructed with material with similar coloration (to the human eye) likely reduces their conspicuousness.

The color (wavelengths) reflected by the silk of the egg sacs of spiders has likely evolved to reduce their contrast against their background, thus making their detection more difficult for parasitoids and predators. However, our research provides only an understanding of the spectral properties of egg sacs from a human perspective, but does not indicate how egg saes are perceived by other animals (e.g., predators and parasitoids). At least two other aspects, the ambient light available for reflection and the nature of the background, also affect the perception of the color and thus the conspicuousness of an object (e.g., egg sac: Théry 2006), independent of the color vision of predators and/or parasitoids. Hence, even when egg sacs have, for instance, high UV reflectance, they could be difficult to detect in low light environments even for those animals capable of seeing UV light. This is the case for *K. hibernalis* whose webs are built in dark locations and the egg sac retained inside a dense silk tunnel, and also for *Deinopis* sp. that construet and leave the egg sacs "unprotected" in the undergrowth of either dense or relatively clear forests (Table 1). *Zosis geniculata* maintains the egg sacs attached to its web until the emergence of the spiderlings, and the silk of the egg sacs has a low UV reflectance, in contrast to web silk of the family (Uloboridae) (Craig et al. 1994; Bond & Opell 1998). This spider inhabits dark environments where webs may be inconspicuous despite high UV reflectance, and the low UV reflectance of its egg sacs likely further reduces conspicuousness. In environments with considerable ambient light, the brightness of the egg sac silk may also reduce its conspicuousness. For instance, *A. pacificus* builds its web and egg sacs in bright, open environments (Agnarsson et al. 2006); thus, the high brightness and low UV reflectance of the egg sacs may reduce its contrast and conspicuousness in open, bright environments. Other theridiids that inhabit bright environments produce egg sac silk with low UV reflectance and reduce the contrast and conspicuousness of their egg sacs by retaining them inside retreats that to the human eye resemble the egg sacs in coloration. Though our data are insufficient to test these hypotheses, they suggest that evolution of coloration in egg sacs of spiders is affected by several aspects of their ecology: the physical properties of the silk that each spider produces, environmental light, and the behavior and natural history of each spider species.

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LITERATURE CITED

Agnarsson, I. 2004. Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae). Zoological Journal of Linnean Society 141:447–626.

Agnarsson, I., G. Barrantes & L.J. May-Collado. 2006. Notes on the biology of *Anelosimus pacificus* Levi, 1963 (Theridiidae, Araneae) – evidence for an evolutionary reversal to a less social state. Journal of Natural History 40:2681–2687.

Aisenberg, A., C. Toscano-Gadea & S. Ghione. 2011. Guía de arácnidos del Uruguay. Editorial de la Fuga, Montevideo, Uruguay.

Austin, A.D. 1985. The function of spider egg sacs in relation to parasitoids and predators, with special reference to the Australian fauna. Journal of Natural History 19:359–376.

Barrantes, G. 2007. Camouflage in webs of *Helvibis longicauda* (Araneae: Theridiidae). Bulletin of the British Arachnological Society 14:59–60.

Barrantes, G. 2008. Courtship behavior and copulation in *Tengella radiata* (Araneae, Tengellidae). Journal of Arachnology 36:606–608.

Bond, J.E. & B.D. Opell. 1999. Testing adaptive radiation and key innovation hypotheses in spiders. Evolution 52:403–414.

Bristowe, W.S. 1958. The World of Spiders. Collins, London.

Coddington, J.A. 1986. The genera of the spider family Theridiosomatidae. Smithsonian Contributions to Zoology 422:1–96.

Craig, C.L. 2003. Spider Webs and Silk. Tracing Evolution from Molecules to Genes to Phenotypes. Oxford University Press, New York.

Craig, C.L., G.D. Bernard & J.A. Coddington. 1994. Evolutionary shifts in the spectral properties of spider silks. Evolution 48:287–296.

Craig, C.L., R.S. Weber & G.D. Bernard. 1996. Evolution of predator prey systems: spider foraging plasticity in response to the visual ecology of prey. American Naturalist 147:205–229.

Eberhard, W.G. 2001. Trolling for water striders: active searching for prey and the evolution of reduced webs in the spider *Wendilgarda* sp. (Araneae, Theridiosomatidae). Journal of Natural History 35:229–251.

Eberhard, W.G. 2003. Substitution of silk stabilimenta for egg sacs by *Allocyclosa bifurca* (Araneae: Araneidae) suggests that silk stabilimenta function as camouflage devices. Behaviour 140:847–868.

Endler, J.A. 1993. The color of light in forests and its implications. Ecological Monographs 63:1–27.

Foelix, R. 2011. Biology of Spiders. Third edition. Oxford University Press, New York.

Gertch, W.J. 1949. American Spiders. Van Nostrand, Princeton, New Jersey.

Herberstein, M.E., C.L. Craig, J.A. Coddington & M.A. Elgar. 2000. The functional significance of silk decorations of orb-web spiders: a critical review of the empirical evidence. Biological Reviews 75:649–669.

Hieber, C.S. 1985. The "insulation" layer in the cocoons of *Argipoe aurantia* (Araneidae: Araneae). Journal of Thermal Biology 10:171–175.

Hieber, C.S. 1992a. The role of spider cocoons in controlling desiccation. Oecologia 89:442–448.

Hieber, C.S. 1992b. Spider cocoons and their suspension systems as barriers to generalist and specialist predators. Oecologia 91:530–535.

Levi, H.W. 1962. The spider genera *Steatoda* and *Enoplognatha* in America (Araneae, Theridiidae). Psyche 69:11–36.

Maia, R., C.M. Eliason, P.-P. Bitton, S.M. Doucet & M.D. Shawkey. 2013. pavo: an R package for the analysis, visualization and organization of spectral data. Methods in Ecology and Evolution: DOI: 10.1111/2041-210X.12069

Montgomerie, R. 2006. Analyzing colors. Pp. 90–147. *In* Bird Coloration, Mechanisms and Measurements. (G.E. Hill & K.J. McGraw, eds.). Harvard University Press, Cambridge, Massachusetts.

Moya, J., R. Quesada, G. Barrantes, W.G. Eberhard, I. Escalante, C. Esquivel, A. Rojas, E. Triana & A. Arias. 2010. Egg sac construction in folded dead leaves by *Pozonia nigroventris* and *Micrathena* sp. (Araneae, Araneidae). Journal of Arachnology 38:371–373.

Nielsen, E. 1932. The Biology of Spiders. Levin & Munkgaard, Copenhagen.

Opell, B.D. 1989. Do female *Miagrammopes animotus* (Araneae, Uloboridae) spin color-coordinated egg sacs? Journal of Arachnology 17:108–111.

Théry, M. 2006. Effects of light environment on color communication. Pp. 148–173. *In* Bird Coloration, Mechanisms and Measurements. (G.E. Hill & K.J. McGraw, eds.). Harvard University Press, Cambridge, Massachusetts.

Triana, E., G. Barrantes & P. Hanson. 2012. Incidence of parasitoids and predators on eggs of seven Theridiidae species (Araneae). Bulletin of the British Arachnological Society 15:293–298.

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No evidence for a relationship between hemolymph ecdysteroid levels and female reproductive behavior in *Schizocosa* wolf spiders

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Abstract. This study used radioimmunoassay (RIA) to explore the relationship between levels of hemolymph ecdysteroids and female reproductive behavior in *Schizocosa* wolf spiders. Specifically, we investigated the relationship between circulating ecdysteroid concentrations in females and 1) likelihood to copulate, or female receptivity [Experiment 1— *Schizocosa avida* (Walckenaer 1837)], 2) time post copulation (Experiment 2— *Schizocosa rovneri* Uetz & Dondale 1979) and 3) exposure to conspecific male courtship (Experiment 3— *Schizocosa uetzi* Stratton 1997). In Experiment 1, we expected higher levels of circulating ecdysteroids in receptive versus unreceptive females, based upon prior research demonstrating an increase in receptivity following injections of 20-hydroxyedysone (e.g., *Tegenaria atrica* C.L. Koch 1843). In contrast, we found no relationship between female receptivity and ecdysteroid levels. Our second experiment compared ecdysteroid levels in mated versus virgin females at three time points following mating trials (24 h, 7 d and 14 d). We predicted low and constant ecdysteroid levels, independent of both mating status and time post mating trial—our results support this prediction. Our third experiment explored the relationship between exposure to conspecific courtship and ecdysteroid levels; again, we found no relationship. Thus, circulating ecdysteroid concentrations were not associated with any aspect of reproductive biology we explored. However, we found a negative trend between female age post maturation and circulating ecdysteroid concentration in the species for which we had the greatest age range, consistent with its role as a molting hormone.

Keywords: 20-hydroxyecdysone, female choice, oogenesis, vitellogenesis

An animal's behavior is the result of complex interactions between a variety of internal (e.g., physiological state) and external (e.g., past environmental conditions) factors. In arthropods, hormones, in particular juvenile hormone and ecdysteroids, commonly act as important mediators of such complex interactions. Previous research focusing on a variety of arthropod groups demonstrates that hormone levels can influence aggression, social interactions and dominance status (American lobster *Homarus americanus*: Bolingbroke & Kass-Simon 2001; cockroach *Nauphoeta cinerea*: Kou et al. 2009; paper wasps *Polistes gallicus*: Röseler et al. 1984; bumble bees *Bombus terrestris*: Bloch et al. 2000); sexual receptivity (insects: Ringo 1996); as well as parental care (burying beetles *Nicrophorus* spp.: Scott & Panaitof 2004). Ecdysteroid-regulated behaviors are often associated with particular stages of development. For example, exogenously applied 20-hydroxyecdysone (20E) at late pre-ecdysis causes female lobsters to become more aggressive, which is similar to their natural premolt behavior (Bolingbroke & Kass-Simon 2001).

Despite the vast amount of knowledge that has been accumulated regarding the relationship between hormones and behavior in insects and crustaceans, our knowledge of the function of hormones in arachnids is relatively limited. Non-spider arachnid studies have focused mostly upon ticks (Ixodoidea) (Germond et al 1982; Bouvier et al. 1982) and opilionids (Opilionidae) (Romer & Gnatzy 1981). Recent investigations across various spider families have suggested that ecdysteroids play a role in reproductive physiology and behavior including regulation of ovarian development and vitellogenesis (Trabalon et al. 1998, 1992; Pourié & Trabalon 2003), pheromone production and cannibalistic interactions (Trabalon et al. 1998, 2005) and sexual receptivity (Trabalon et al. 2005). To date, ecdysteroids have been studied in only a handful of spider species: e.g., *Coelotes terrestris* (Wider 1834); *Tegenaria domestica* (Clerck 1757) (Trabalon et al. 1992); *Pisaura mirabilis* (Clerck 1757) (Bonnaric and De Reggi 1977); *T. atrica* (C.L. Koch 1837) (Trabalon et al. 1998) and *Brachypelma albopilosum* Valerio 1980 (Trabalon & Blais 2012).

Here we quantify hemolymph ecdysteroid levels in *Schizocosa* wolf spiders. The adult morphology and associated courtship behavior of male *Schizocosa* vary widely and are often complex, containing both visual ornaments and movements as well as seismic courtship components (reviewed in Stratton 2005; Framenau & Hebets 2007; Vaccaro et al. 2010; Hebets et al. 2013). This genus has been at the forefront of studies of sexual selection via female mate choice, secondary sexual trait evolution and function, and complex signaling (reviewed in Uetz & Roberts 2002; Hebets et al. 2011, 2013; Rundus et al. 2011). Information gained regarding putative mechanistic underpinnings of female reproductive behavior would add significantly to our knowledge of basic reproductive physiology in this well-studied system. Additionally, the genus *Schizocosa* encompasses one of the first arthropod species for which an effect of subadult experience on subsequent mate choice behavior has been demonstrated (Hebets 2003; Hebets & Vink 2007), making species in the genus a good choice for studies addressing potential effects of female experience on reproductive behavior and physiology.

We used three species of *Schizocosa* readily available to us in the laboratory [*Schizocosa avida* (Walckenaer 1837), *S. rovneri* Uetz & Dondale 1979 and *S. uetzi* Stratton 1997] to investigate the relationship between hemolymph ecdysteroid levels and female reproductive behavior and experience. Our

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Table 1.—Collection information for *Schizocosa* species.

	Collection Sites	Collection Time	GPS Coordinates
S. avida	Lancaster CO, NE USA	June & July 2007 & 2008	40.749, −96.817
S. rovneri	Lafeyette CO, MS USA	10–11 April 2010	34.431, −89.706
S. uetzi	Lafeyette CO, MS USA	21–22 May 2007	34.431, −89.706

first experiment tested the hypothesis that female reeeptivity is associated with heightened levels of hemolymph ecdysteroids. Our second experiment tested the hypothesis that hemolymph ecdysteroids remain stable following copulation, despite the likely transition from pre-vitellogenesis to vitellogenesis. Finally, our third experiment explored the possibility that exposure to conspecific male courtship influences hemolymph ecdysteroid levels.

Our first experiment builds upon prior work in other spider groups. Ecdysteroid levels are known to increase sharply in females following their final maturational molt; in *C. terrestris* and *T. domestica*, this happens 10–30 days post maturation (Trabalon et al. 1992). This increase in hemolymph ecdysteroids coincides with the transition between the pre-vitellogeneic and early vitellogeneie phase of oocyte development in virgin females (Trabalon et al. 1992, 1998). This natural increase may also coincide with increased female receptivity, as some females exhibit peak receptivity at ~ 3 weeks post maturation (e.g., *Schizocosa ocreata* (Hentz 1844): Uetz & Norton 2007). Additionally, prior hormone manipulation work is consistent with the hypothesis that an increase in receptivity is associated with increased ecdysteroid levels. Following an injection of 20E in *T. atrica,* females showed an increase in the frequency of sexual receptivity (Trabalon et al. 2005).

Our second experiment aimed to examine the influence of mating on ecdysteroid levels by quantifying hemolymph ecdysteroid levels at various time points post-copulation. We predieted that ecdysteroid levels would be relatively low in mated females and would be independent of time post mating (i.e., levels would remain stable). The maturation of ovaries in spiders occurs in three phases: 1) a pre-vitellogenic phase, 2) a vitellogenic phase, and 3) a post-vitellogenie phase (Andre and Rouiller 1957; Sotelo and Trujillo-Cenoz 1957; Trabalon et al. 1992), with six distinct stages described (Trabalon et al. 1992). Late vitellogenesis and post-vitellogenesis (stages 5–6) have only been observed in mated females and appear to be associated with relatively low and constant hemolymph ecdysteroid levels (Trabalon et al. 1992), and the highest levels of hemolymph ecdysteroids are found in virgin versus mated females (Trabalon et al. 1998).

Our final experiment builds upon previous behavioral work showing that the mate choice of *Schizocosa* females can be altered after exposure to courtship advances from conspecific males (Hebets 2003, Hebets & Vink 2007). *Schizocosa uetzi* was chosen as the focal species for the third experiment, since it is in this species that an effect of subadult experience on adult mate choice was first demonstrated (Hebets 2003). Given the previously demonstrated effect of exogenously injected 20E on sexual receptivity in *T. atrica* (Trabalon et al. 2005), we hypothesized that variation in ecdysteroids underlies this previously observed mate choice preference. If so, we predicted that females exposed to male courtship would have higher levels of hemolymph ecdysteroids than unexposed females.

METHODS

General methods.—All spiders were collected as subadults (Table 1) and were housed individually in visually isolated plastic containers placed together in large plastic tubs filled with water (see Rundus et al. 2011). Spiders were provided crickets (*Acheta domesticus*) twice a week. To the best of our knowledge, all three species of *Schizocosa* used in this study have a one-year life cycle with maturation molts oecurring in late spring/early summer. Egg sacs are laid in mid-summer and overwintering occurs at the juvenile stages.

Experiment 1: Female receptivity and ecdysteroids (*Schizocosa avida*).—We chose *S. avida* as the focal species for this first experiment as it is a relatively large species within the genus (Dondale & Redner 1978), which enabled us to take hemolymph samples from individuals prior to mating trials. All individuals survived our collection technique. This was important because our aim was to examine the relationship between eedysteroid levels and subsequent likelihood to copulate. This speeies was locally abundant and thus readily available. Twenty-eight mature female *S. avida* spiders ranging in age from 3–35 days post-maturation (mean ± SE = 21.9 ± 1.89) were used in receptivity trials. We purposefully included a wide range of ages to examine age-related variation in ecdysteroid levels simultaneously. Females were weighed two days prior to receptivity trials, hemolymph was collected via bleeding (see "Hemolymph Collection") and individuals were returned to their containers. After two days of recovery, females did not display any noticeable aberrant behaviors.

Females were placed in a circular plastic arena (radius: 11.5 cm, height: 7.5 cm) two days post bleeding and were allowed to acclimate and lay silk on a piece of filter paper lining the bottom of the arena. After 2 h of acclimation, a mature conspecific male was introduced. Females and males were only used once. Each pair was allowed to interact for 30 min. We recorded the presence or absence of eopulation.

Experiment 2: Time post-copulation and ecdysteroids (*Schizocosa rovneri*).—Fifty-eight mature virgin female *S. rovneri* ranging in age from 10–39 days post maturation (mean ± SE = 21.4 ± 0.96) were used in mating trials with mature virgin conspecific males. We had no a priori reason to use *S. rovneri* for this experiment, but took advantage of their availability in the laboratory due to other ongoing studies. Individual males and females were only used once. Our design enabled us to determine whether hemolymph ecdysteroid levels would change following copulation, as we compared these levels between mated and unmated females at three time points post mating trials (and thus, post eopulation for mated females). Mating trials were run in cireular arenas exactly as in Experiment 1. If copulation occurred, the pair was left

undisturbed until it ended. If no copulation occurred, the female was returned to her home container. We collected hemolymph from females (mated and unmated) at three randomly assigned time points following mating trials: 24 h, 7 d or 14 d. We collected hemolymph only onee from each female. All females were weighed before bleeding and bleeding occurred at the same time of day as the original mating trials ±2 h (see "Hemolymph Collection").

Of the 58 females used in this experiment, 29 copulated. We collected hemolymph from 15 females at 24 h post mating trial (copulation = 5, no copulation = 10); from 17 females at 7 d post mating trial (copulation = 8, no copulation = 9) and from 26 females at 14 d post mating trial (copulation = 16, no copulation = 10).

Experiment 3: Courtship exposure and ecdysteroids (*Schizocosa uetzi*).—To explore the relationship between exposure to male courtship and hemolymph ecdysteroids, we compared ecdysteroid levels of virgin females exposed versus unexposed to male courtship. Since subadult female *S. uetzi* respond to exposure to eonspeeific male courtship (Hebets 2003), we chose this as our focal species. Forty-six mature females ranging in age from 35–55 days post maturation molt (mean ± SE = 42.9 ± 0.69) were used.

Females were assigned to one of two treatments: 1) exposure to conspecific male courtship (exposed; n = 30) or 2) no exposure to conspeeific male courtship (unexposed; n = 16). At the start of a trial, a female was allowed to acclimate for 15 min in a plastic arena (8.8 cm × 8.8 cm × 11 em) lined with filter paper to enable seismic cue transmission. The arena had its sides covered with masking tape to provide visual isolation from the surrounding room. For exposed females, following the acclimation period a thin circular transparent acetate barrier (radius: 3 cm, height: 5 cm) was lowered around the female, enclosing her in the center of the larger arena. A mature conspecific male was then placed in the surrounding arena, and the pair was observed for 30 min. During this period females were exposed to male visual and seismic courtship signals, but could not contact the males. For unexposed females, an identical thin transparent acetate barrier was lowered after the 15 min acclimation period, enclosing the female for 30 min, but no male was introduced in the larger arena. Females were bled immediately following their trial; no more than 5 min passed between trial ending and hemolymph collection (see "Hemolymph Collection").

Hemolymph collection.—Each spider was weighed and placed in a quart-sized Ziploc plastic bag that had one corner cut. Spiders were positioned in the bag such that one leg could protrude through the opening in the cut corner. This leg was then cut in the middle of the femur and hemolymph was collected in glass micropipettes. If 10 µL could not be obtained from the first cut, a second leg was cut. In some cases less than 10 µL of hemolymph were colleeted. Hemolymph samples were blown into microcentrifuge tubes containing 300 µL of 90% methanol. Tubes were vortexed for ~5 s and stored in a −20 °C freezer until ecdysteroids were assayed.

Radioimmunoassay analysis.—Total ecdysteroid concentration was estimated from three replicates of each hemolymph sample using a standard radioimmunoassay similar to that described in Zera and Bottsford (2001). 20E was used as the standard. Briefly, a small sample of hemolymph extract or ecdysteroid standard was added to a test tube, solvent was evaporated under a gentle stream of nitrogen and 100 µL of diluted anti-ecdysteroid polyclonal antiserum in 0.1 M borate buffer containing 75 mM NaCl (pH 8.3) was added. The antiserum had been produced in the laboratory of W. E. Bollinbacher (University of North Carolina, Chapel Hill) and was provided by E. S. Chang (Bodega Marine Laboratory, Bodega Bay, California). Subsequently, 5000 CPM ecdysone (Ecdysone α-[23,24-^{3}H(N)], PerkinElmer Inc., Boston, MA) in 100 µL borate buffer was added. Tubes were vortexed for ~5 s and incubated overnight at 4 °C.

The next day, 50 µL of a 10 mg/mL bovine gamma globulin solution (co-precipitant) in borate buffer was added to each tube, followed by 250 µL of saturated aqueous ammonium sulfate ($(NH_4)_2SO_4$) to precipitate the antibody-ecdysteroid complex. Tubes were vortexed for ~5 s, incubated on ice for 30 min and centrifuged at 5000 RPM for 10 min at 4 °C. The supernatant was removed and 250 µL of 50% saturated $(NH_4)_2SO_4$ in borate buffer was added to each tube, which was vortexed and centrifuged as above. Both sets of supernatants were discarded and the pellets (containing antibody plus bound ecdysteroid) were dissolved in 500 µL of borate buffer, transferred to plastic scintillation vials and counted on a 1450 MicroBeta TriLux Liquid Scintillation Counter (PerkinElmer, Boston, MA). Ecdysteroid concentrations in hemolymph samples were estimated by standard nonlinear regression using Prism GraphPad Version 4. Standard curves were constructed from the following 20E masses (0.02, 0.07, 0.2, 0.7 and 2 ng), all of which gave r^2 values greater than 0.99 with the exception of one at r^2 = 0.9661. Back calculations were used to determine the ecdysteroid concentration from the interpolated masses in hemolymph samples based on standard curves generated during each assay.

Statistical analyses.—For all three experiments we examined the relationship between our predictor variables (treatment and age) and the response variable (measured concentration of ecdysteroids), using least squares regression analyses. In all instances we first ran a full model with all possible interactions and included female weight as a predictor variable. We found no significant interactions and no effect of female weight and thus we report only our reduced models. All analyses were eonducted in JMP (Version 8). To conform to assumptions of normality, we used a natural log (ln) transformation of our response variable, ecdysteroid concentration.

Effect sizes were calculated using from the P-values of our models with the following website: http://www.campbellcollaboration.org/resources/effect_size_input.php.

RESULTS

None of our least squares regression models were significant. Receptivity did not predict ecdysteroid levels in *S. avida* ($F_{3,21}$ = 1.84, P = 0.17, Fig. 1). Neither mating status (copulated vs. virgin), time post mating trial, nor an interaction between the two, predicted ecdysteroid levels in *S. rovneri* ($F_{6,51}$ = 0.72, P = 0.64, Fig. 2). Experience with a conspecific male in *S. uetzi* had no influence on hemolymph ecdysteroid levels ($F_{3,42}$ = 0.64, P = 0.59, Fig. 3). Ultimately, we found no evidence of a relationship between our measured concentration of ecdysteroids in the hemolymph and any of our examined aspects of reproductive behavior. Details of

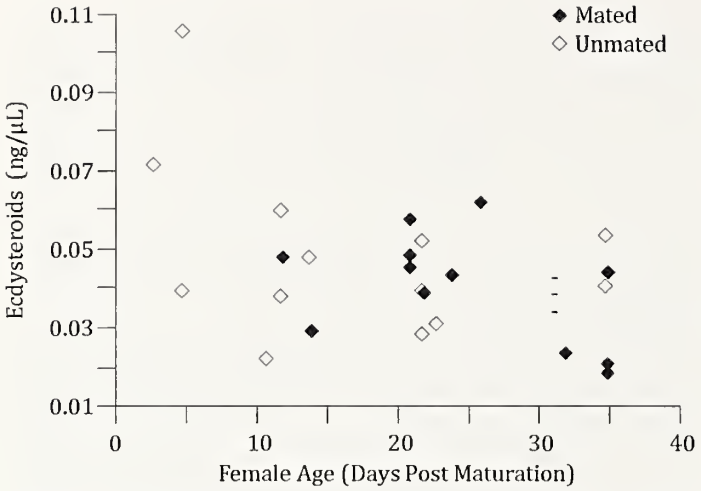

Figure 1.—Hemolymph ecdysteroid concentrations of *S. avida* females of different ages. There was a negative trend of decreasing ecdysteroid concentration with increasing age ($P = 0.05$). This trend was largely driven by a single female. The three dashes represent individuals whose copulation status was not tested.

each of our models can be seen in Table 2. Younger *S. avida* females had ecdysteroid levels that were nearly significantly higher than those of older females (see Table 2; $r^2 = 0.20$, $P = 0.05$, Fig. 1). A single female appeared to be largely responsible for this near significance (Fig. 1).

DISCUSSION

This study reports the first naturally occurring levels of ecdysteroids in the hemolymph of *Schizocosa* wolf spiders. Observed levels were comparable to concentrations detected previously using enzyme immunoassay in adult spiders of *Tegenaria domestica* (0.00441–0.01767 ng/μL), *Coelotes terrestris* (0.00071–0.02528 ng/μL) (Trabalon et al. 1992), *Tegenaria atrica* (0.00747–0.01345 ng/μL) (Trabalon et al. 1998) and

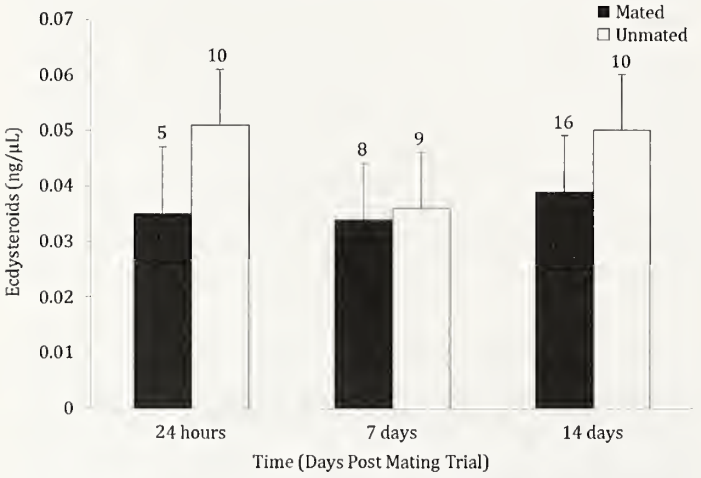

Figure 2.—Comparison of hemolymph ecdysteroid concentrations in *S. rovneri* mated versus unmated females at 24 h, 7 d and 14 d after mating trials. The bars represent the average hemolymph ecdysteroid concentration, and the error bars represent the standard error. There was no significant difference in ecdysteroid concentration between mated and unmated females ($P = 0.21$) or time post trial ($P = 0.11$). The numbers above the bars indicate sample sizes.

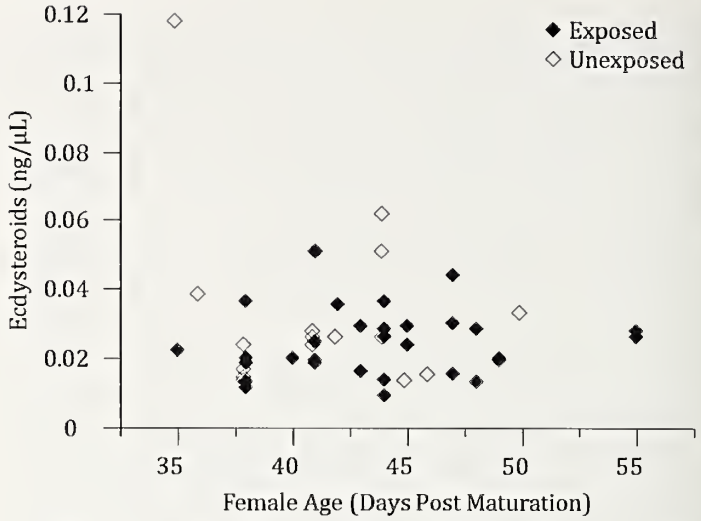

Figure 3.—Hemolymph ecdysteroid concentrations in *S. uetzi* females exposed or unexposed to conspecific male courtship. There was no significant difference in ecdysteroid concentration between courtship treatment (exposed versus unexposed) ($P = 0.37$), age ($P = 0.85$), or the interaction of these variables ($P = 0.41$).

Brachypelma albopilosum (females: 0.00744 ng/μL, males: 0.01122 ng/μL) (Trabalon & Blais 2012). We found no relationship between ecdysteroids and reproductive behavior in the *Schizocosa* species tested. Specifically, we found no relationship with 1) likelihood to copulate (i.e., female receptivity) (Exp. 1 – *Schizocosa avida*); 2) time post copulation (Exp. 2 – *Schizocosa rovneri*) or 3) female exposure to conspecific courtship (Exp. 3 – *Schizocosa uetzi*). Our calculated effect sizes (denoted *r*, Table 2) were not particularly large, indicating that our lack of significance was probably not attributable to low sample sizes.

In our first experiment, we predicted higher levels of hemolymph ecdysteroids in receptive versus unreceptive *S. avida* females, but we found no indication that receptivity was a good predictor of hemolymph ecdysteroid levels. Our expectations were based upon prior work in other spiders showing high ecdysteroid levels 10–30 days post maturation and in 20 day old virgin females (Trabalon et al. 1992, 1998)—a time during which *Schizocosa* females are known to show peak receptivity (Uetz & Norton 2007). In contrast to our prediction, our results indicate a trend towards an immediate decrease in hemolymph ecdysteroids following maturation (Fig. 1), consistent with a role in molting. Regardless, we did not detect a surge in hemolymph ecdysteroids in virgin females 10–30 days post maturation. It is important to note that in addition to the fact that *Schizocosa* wolf spiders (Family Lycosidae) are not close relatives of the previously studied spider species (e.g., *Coelotes*, Family Amaurobiidae; *Tegenaria*, Family Agelenidae), the method of collecting hemolymph samples also varied across studies. In *C. terrestris*, *T. domestica*, and *T. atrica*, hemolymph was collected from the thorax with glass microcapillary tubes. In contrast, our hemolymph (present study) was collected in glass microcapillary tubes from clipped walking legs. Given the proximity of the hemolymph collection site in the prior studies to the central nervous system of the spider, it is possible that ecdysteroid levels in the prosoma (a potential location for

Table 2.—Mean hemolymph ecdysteroid levels for all species and results of least squares regression models. Experiment 1 compared ecdysteroid levels between females that did and did not copulate. Experiment 2 compared ecdysteroid levels between females that did and did not copulate across time points. Experiment 3 compared ecdysteroid levels between females exposed and unexposed to male courtship.

Experiment	Ecdysteroid Mean ± SE (ng/μL)	Effect	F Ratio	P value	*r*	CI
Exp. 1 (*S. avida*)	0.04 ± 0.003	Female age	4.29	0.05	0.39	−0.003–0.66
		Copulation (yes/no)	0.01	0.91	0.02	0.37–0.42
		Age * Copulation	0.73	0.4	0.18	−0.24–0.53
Exp. 2 (*S. rovneri*)	0.042 ± 003	Female age	0.49	0.49	0.09	−0.17–0.34
		Copulation (yes/no)	2.48	0.12	0.21	−0.05–0.44
		Time Treatment	0.85	0.43	0.11	−0.16–0.35
Exp. 3 (*S. uetzi*)	0.027 ± 0.002.5	Female age	0.035	0.85	0.03	−0.26–0.32
		Courtship Treatment	0.82	0.37	0.14	−0.16–0.41
		Age * Courtship	0.69	0.41	0.12	−0.17–0.40

ecdysteroid synthesis) are not equivalent to levels circulating in the walking legs. Additionally, although prior work in other species clearly demonstrated an increase in ecdysteroid concentrations 10–30 days post maturation, this was correlated with timing of oocyte development, specifically with the transition between pre-vitellogenesis and early vitellogenesis (see below). In *Schizocosa*, the timing of this transition is currently unknown. Finally, the strongest evidence for a link between receptivity and ecdysteroid levels comes from a hormone manipulation study. In *T. atrica,* females were injected with 2 ng of 20E in 1 μL of Ringer's solution and showed an increase in reeeptivity. Such a concentration was expected to result in a hemolymph concentration of 0.5 ng/μL, which is much higher than that found in unmanipulated individuals (Trabalon et al. 2005). This large dose of hormone was presumed necessary, as 20E is rapidly degraded in other spiders (Connat et al. 1988). However, the unnaturally high hormone dose administered may have caused the observed behavioral changes in these spiders. Incidental (non-physiological) side-effects of hormone injection are not uncommon in hormone studies of invertebrates (Zera 2007). Given the results of the previous hormone manipulation study and the suggestion of a relationship between 20E and receptivity in *T. atrica,* this species would be ideal for directly testing the hypothesis that circulating ecdysteroid levels are correlated with receptivity behavior.

In spiders, vitellogenesis does not occur until females have copulated, yet Pourié & Trabalon (2003) were able to induce vitellogenesis in virgin females through injections of 20E, suggesting its role in vitellogenesis. However, all assays of hemolymph ecdysteroid levels in mated females indicate that ecdysteroid levels are constant and low following copulation (Trabalon et al. 1992, 1998). The results of our second experiment are consistent with these earlier findings, as our measured ecdysteroid levels in *S. rovneri* did not vary according to their mating status (mated versus virgin), their time post mating trial (24 h, 7 d, 14 d) or an interaction between the two (Fig. 2). One potential explanation for these results is that ecdysteroids are not involved in vitellogenesis in these spiders. This would not be unprecedented, as not all insects use ecdysteroids to initiate vitellogenesis [e.g., lubber grasshopper *Romalea microptera* (Hatle et al. 2003); cockroach *Leucophaea maderae* (Engelmann 2002)]. Alternatively, and potentially more likely, levels of ecdysteroids circulating in the hemolymph of the walking legs may not be the most relevant measures for their role in vitellogenesis. In insects, ecdysteroidogenesis occurs in the gonads, and in non-insect arthropods this process occurs in specialized tissues or organs (e.g., the Y-organ in crustaceans) and ecdysteroids are trafficked to the gonad via lipoproteins such as vitellogenin (Brown et al 2009). Thus, measurement of ovarian 20E concentrations may reveal differences between mated and non-mated females.

Finally, our last experiment was an exploratory endeavor to determine whether there might be a relationship between a female's prior experience with a courting conspecific male and ecdysteroid levels. Given that we found no relationship between female receptivity and ecdysteroid levels (Exp. 1), it is not surprising that we similarly failed to find a relationship in this third experiment (Fig. 3). Arguably, our exposures were conducted on relatively old mature virgin females so the possibility remains that exposure earlier in life influences ecdysteroid levels. Further, our assays focused solely on ecdysteroid levels in the hemolymph and, as above, the possibility remains that concentration changes take place in specific tissues or organs, such as the ovary.

Early investigations in spiders implicated ecdysteroids as molting hormones (reviewed in Krishnakumaran & Schneiderman 1970; Bonaric & Reggi 1977; Bonaric 1987), and our results are consistent with this function. In many arthropod groups, the level of 20E is known to fluetuate over a molt cycle in a predictable pattern [e.g., crustaceans: shore crab *Carcinus maenas* (Styrishave et al. 2008); prawn *Macrobrachium rosenbergii* (Okumura & Aida 2000); isopod (*Armadillidium vulgare*) Suzuki et al. 1996; lobster, *Homarus americanus* Synder & Chang 1991); several orders of insects: termite *Coptotermes formosanus*: Isoptera (Raina et al. 2008); beetle *Zophobas atratus*: Coleoptera (Delbecque et al. 1997); fruit fly *Drosophila melanogaster*: Diptera (Handler 1982); arachnids: tick *Ornithodoros moubata* (Germond et al. 1982); spiders *Pisaura mirabilis* (Bonaric & Reggi 1977; Bonaric 1987). Typically, ecdysis, or the final shedding of the cuticle, occurs shortly after 20E concentration begins to decrease from its peak concentration, ultimately returning to its baseline level. This is a similar pattern to what we observed in *S. avida,* the only species for which we have data on females immediately following their maturation molt.

In summary, we quantified the concentration of ecdysteroids in three species of *Schizocosa* wolf spiders encompassing a variety of reproductive behaviors. We found no evidence for a relationship between hemolymph ecdysteroid levels and

female reproductive behavior. Given that ecdysteroid synthesis and secretion are often organ-specific in other arthropod groups, however, it is possible that our measures of circulating hemolymph ecdysteroids did not capture ecdysteroid concentrations pertinent to our focal reproductive behavior. Our results are consistent with ecdysteroids acting as the molting hormone in these spiders, but suggest that circulating levels do not act significantly in female mating behavior or reproductive physiology.

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LITERATURE CITED

Andre, J. & C. Rouiller. 1957. The ultrastructure of the vitelline body in the oocyte of the spider *Tegenaria parietina*. Journal of Biophysical and Bioehemical Cytology 3:977–984.

Bloch, G., A. Hefetz & K. Hartfelder. 2000. Ecdysteroid titer, ovary status, and dominance in adult worker and queen bumble bees (*Bombus terrestris*). Journal of Insect Physiology 46:1033–1040.

Bolingbroke, M. & G. Kass-Simon. 2001. 20-hydroxyecdysone causes increased aggressiveness in female American lobsters, *Homarus americanus*. Hormones and Behavior 39:144–156.

Bonaric, J.C. 1987. Moulting hormones. Pp. 111–118. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer-Verlag, Berlin.

Bonaric, J.C. & M. De Reggi. 1977. Changes in ecdysone levels in the spider *Pisaura mirabilis* nymphs (Araneae, Pisauridae). Experientia 33:1664–1665.

Bouvier, J., P.A. Diehl & M. Morici. 1982. Ecdysone metabolism in the tick *Ornithodoros moubata* (Argasidae, Ixodoidea). Revue Suisse de Zoologie 89:967–976.

Brown, M.R., D.H. Sieglaff & H.H. Rees. 2009. Gonadal ecdysteroidogenesis in Arthropoda: occurrence and regulation. Annual Review of Entomology 54:105–125.

Connat, J.L., P.A. Fürst & M. Zweilin. 1988. Detoxification of injected and ingested ecdysteroids in spiders. Comparative Biochemistry and Physiology B 91:257–265.

Delbecque, J., N. Pitoizet, A. Quennedey & N. Aribi. 1997. Ecdysteroid titres in a tenebrionid beetle, *Zophobas atratus*: effects of grouping and isolation. Journal of Insect Physiology 43:815–821.

Dondale, C.D. & J.H. Redner. 1978. Revision of Nearctic wolf spider genus *Schizocosa* (Araneida: Lycosidae). Canadian Entomologist 110:143–181.

Engelmann, F. 2002. Ecdysteroids, juvenile hormone and vitellogenesis in the cockroach *Leucophaea maderae*. Journal of Insect Science 2:20.

Framenau, V.W. & E.A. Hebets. 2007. A review of leg ornamentation in male wolf spiders, with the description of a new species from Australia, *Artoria schizocoides* (Araneae, Lycosidae). Journal of Arachnology 35:89–101.

Friesen, K.J. & W.R. Kaufman. 2002. Quantification of vitellogenesis and its control by 20-hydroxyecdysone in the ixodid tick, *Amblyomma hebraeum*. Journal of Insect Physiology 48: 773–782.

Germond, J.E., P.A. Diehl & M. Morici. 1982. Correlations between integument structure and ecdysteroid titers in fifth-stage nymphs of the tick *Ornithodoros moubata* (Murray 1877; sensu Walton 1962). General and Comparative Endocrinology 46:255–266.

Handler, A.M. 1982. Ecdysteroid titers during pupal and adult development in *Drosophila melanogaster*. Developmental Biology 93:73–82.

Hatle, J.D., Juliana, S.A. & D.W. Borst. 2003. Hemolymph ecdysteroids do not affect vitellogenesis in the lubber grasshopper. Archives of Insect Biochemistry and Physiology 52:45–57.

Hebets, E.A. 2003. Subadult experience influences adult mate choice in an arthropod: exposed female wolf spiders prefer males of a familiar phenotype. Proceedings of the National Academy of Sciences 100:13390–13395.

Hebets, E.A. & C.J. Vink. 2007. Experience leads to preference: experienced females prefer brush-legged males in a population of syntopic wolf spiders. Behavioral Ecology 18:1010–1020.

Hebets, E.A., C.J. Vink, L. Sullivan-Beckers & M.F. Rosenthal. 2013. The dominance of seismic signaling and selection for signal complexity in *Schizocosa* multimodal courtship displays. Behavioral Ecology and Sociobiology. In press.

Hebets, E.A., J.A. Stafstrom, R.L. Rodriguez & D.J. Wilgers. 2011. Enigmatic ornamentation eases male reliance on courtship performance for mating success. Animal Behaviour 81:963–972.

Kou, R., S.Y. Chou, S.C. Chen & Z.Y. Huang. 2009. Juvenile hormone and the ontogeny of cockroach aggression. Hormones and Behavior 56:332–338.

Krishnakumaran, A. & H.A. Schneiderman. 1970. Control of molting in mandibulate and chelicerate arthropods by ecdysones. Biological Bulletin 139:520–538.

Okumura, T. & K. Aida. 2000. Fluctuations in hemolymph ecdysteroid levels during the reproductive and non-reproductive molt cycles in the giant freshwater prawn *Macrobrachium rosenbergii*. Fisheries Science 66:876–883.

Parthasarathy, R., Z. Sheng, Z. Sun & S.R. Palli. 2010. Ecdysteroid regulation of ovarian growth and oocyte maturation in the red flour beetle, *Tribolium castaneum*. Insect Biochemistry and Molecular Biology 40:429–439.

Pourié, G. & M. Trabalon. 2003. The role of 20-hydroxyecdysone on the control of spider vitellogenesis. General and Comparative Endocrinology 131:250–257.

Raina, A., Y.I. Park & D. Gelman. 2008. Molting in workers of the Formosan subterranean termite *Coptotermes formosanus*. Journal of Insect Physiology 54:155–161.

Ringo, J. 1996. Sexual receptivity in insects. Annual Review of Entomology 41:473–494.

Romer, F. & W. Gnatzy. 1981. Arachnid oenocytes: ecdysone synthesis in the legs of harvestmen (Opilionidae). Cell and Tissues Research 216:369–391.

Röseler, P.F., I. Röseler, A. Strambi & R. Augier. 1984. Influence of insect hormones on the establishment of dominance hierarchies among foundresses of the paper wasp, *Polistes gallicus*. Behavioral Ecology and Sociobiology 15:133–142.

Rundus, A.S., L. Sullivan-Beckers, D.J. Wilgers & E.A. Hebets. 2011. Females are choosier in the dark: environment-dependent reliance on courtship components and its impact on fitness. Evolution 65:268–282.

Scott, M.P. & S.C. Panaitof. 2004. Social stimuli affect juvenile hormone during breeding in biparental burying beetles (Silphidae: *Nicrophorus*). Hormones and Behavior 45:159–167.

Seixas, A., K.J. Friesen & W.R. Kaufman. 2008. Effect of 20-hydroxyecdysone and haemolymph on oogenesis in the ixodid tick *Amblyomma hebraeum*. Journal of Insect Physiology 54:1175–1183.

Sonobe, H. & R. Yamada. 2004. Ecdysteroids during early embryonic development in silkworm *Bombyx mori*: metabolism and functions. Zoological Science 21:503–516.

Sotelo, J.R. & O. Trujillo-Cenoz. 1957. Electron microscope study of the vitelline body of some spider oocytes. Journal of Biophysical and Biochemical Cytology 25:301–310.

Stratton, G.E. 2005. Evolution of ornamentation and courtship behavior in *Schizocosa*: insights from a phylogeny based on morphology (Araneae, Lycosidae). Journal of Arachnology 33: 347–376.

Styrishave, B., T. Lund & O. Andersen. 2008. Ecdysteroids in female shore crabs *Carcinus maenas* during the moulting cycle and oocyte development. Journal of the Marine Biologieal Assoeiation of the United Kingdom 88:575–581.

Subramoniam, T., R. Tirumalai, V. Gunamalai & K.H. Hoffman. 1999. Embryonic ecdysteroids in a mole crab, *Emerita asiatica*. Journal of Biosciences 24:91–96.

Suzuki, S., K. Yamasaki, T. Fujita, Y. Mamiya & H. Sonobe. 1996. Ovarian and hemolymph ecdysteroids in the terrestrial isopod *Armadillidium vulgare*. General and Comparative Endocrinology 104:129–138.

Synder, M.J. & E.S. Chang. 1991. Ecdysteroids in relation to the molt cycle of the American lobster, *Homarus americanns*. General and Comparative Endocrinology 81:133–145.

Trabalon, M., A.M. Bautz, M. Moriniere & P. Porcheron. 1992. Ovarian development and correlated changes in hemolymphatic ecdysteroid levels in two spiders, *Coelotes terrestris* and *Tegenaria domestica* (Araneae, Agelenidae). General and Comparative Endocrinology 88:128–136.

Trabalon, M. & C. Blais. 2012. Juvenile development, ecdysteroids and hemolymph level of metabolites in the spider *Brachypelma albopilosum* (Theraphosidae). Journal of Experimental Zoology 317:236–247.

Trabalon, M., J. Niogret & C. Legrand-Frossi. 2005. Effect of 20-hydroxyecdysone on cannibalism, sexual behavior, and contact sex pheromone in the solitary female spider, *Tegenaria atrica*. General and Comparative Endocrinology 144:60–66.

Trabalon, M., G. Pourié & N. Hartmann. 1998. Relationships among cannibalism, contact signals, ovarian development and ecdysteroid levels in *Tegenaria atrica* (Araneae, Agelenidae). Insect Biochemistry and Molecular Biology 28:751–758.

Uetz, G.W. & S. Norton. 2007. Preference for male traits in female wolf spiders varies with thc choice of available males, female age, and reproductive state. Behavioral Ecology and Sociobiology 61:631–641.

Uetz, G.W. & J.A. Roberts. 2002. Multisensory cues and multimodal communication in spiders: Insights from video/audio playback studies. Brain, Behavior and Evolution 59:222–230.

Vaccaro, R., G.W. Uetz & J.A. Roberts. 2010. Courtship and mating behavior of the wolf spider *Schizocosa bilineata* (Araneae: Lycosidae). Journal of Arachnology 38:452–459.

Zera, A.J. 2007. Endocrine analysis in evolutionary–developmental studies of insect polymorphism: Use and misuse of hormonal manipulation. Evolution and Development 9:499–513.

Zera, A.J. & J. Bottsford. 2001. The endocrine-genetic basis of life history variation: the relationship between the ecdysteroid titer and morph-specific reproduction in the wing-polymorphic crieket *Gryllus firmns*. Evolution 55:538–549.

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Richness and composition of spiders in urban green spaces in Toledo, Ohio

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Abstract. Urbanization negatively affects biodiversity by increasing disturbance and habitat fragmentation. We compared three different urban habitats (vacant lots, gardens and forests) to examine differences in spider communities. We selected four sites of each habitat type and sampled spiders with pitfall traps. We collected a total of 547 individuals from 19 families. The most common families were Lycosidae, Corinnidae, Liocranidae, Cybaeidae, and Dictynidae. Spider activity-density overall and for males and females was higher in vacant lots than in forests, and female spiders had greater activity-density in gardens than in forests. Observed species richness did not differ with habitat type. Spider family composition differed significantly between urban habitat types, female morphospecies composition differed in forests and gardens and male morphospecies composition differed in forests and lots. The site characteristics differed significantly with habitat, and these habitat differences explained a large fraction (53.3% to 90.9%) of the variation in composition and richness. Yet, bare ground was the only factor that significantly correlated with declines in female richness. Thus, spider communities, aspects of specifically activity-density and composition, differ between habitats in urban green spaces with potentially important implications for conservation and trophic interactions within urban areas.

Keywords: Araneae, biodiversity, habitat fragmentation, urbanization

Urbanization leads to habitat loss and fragmentation, both serious threats to biodiversity. Along with the spread of invasive species, habitat loss is considered the greatest threat to biodiversity (Wilcove et al. 1998). Currently, 3 billion people, 48% of the world's human population, live in urban settings, and urban population size is projected to reach 6 billion (a 200% increase) by 2030, while rural populations are projected to decrease by only 3% (United Nations Information Service 2004). With this projected doubling of urban population an even greater proportion of land will become fragmented. Wildlife has responded to urbanization and fragmentation by adapting, moving, or experieneing population crashes (Markovchick-Nicholls et al. 2008). Although other human activities, such as road building and development of infrastructure fragment habitat, urban development results in local mass extinctions, leading to elimination of many native species (McKinney 2002).

Until recently, the importance of urban habitats for arthropod communities was largely ignored (Miller & Hobbs 2002). However, some studies examined urban to rural gradients as early as 1998, finding that overall carabid beetle diversity did not decline with increasing urbanization along a forested habitat (Magura et al. 2010a). A recent surge of studies has investigated how differences among urban habitat types, differences along an urban to rural gradient, and the landscape in which urban habitats are embedded, affect different arthropod communities (e.g., Turner et al. 2004; Carpaneto et al. 2005; Shochat et al. 2006; Elek & Lövei 2007; Pacheco & Vasconcelos 2007; McKinney 2008; Christie & Hochuli 2009; Uno et al. 2010; Fattorini 2011; Tóthmérész et al. 2011). Most studies have examined arthropod communities across rural-urban gradients (Vilisics et al. 2007; Hornung et al. 2007; Tonietto et al. 2011; Varet et al. 2011), but relatively few have compared arthropod communities in more than one habitat type exclusively within urban settings (Yamaguchi 2004; Rango 2005; Sadler et al. 2006; Smith et al. 2006; Thompson & McLachlan 2007; Cárdenas & Buddle 2009; Uno et al. 2010). As such, there is still a need for more invertebrate studies from within cities.

Spiders are important predatory arthropods and are excellent indicators of habitat modifications and disturbance. Spider communities have been well examined in forest ecosystems (Miyashita et al. 1998; Dias et al. 2006), in agricultural settings (Riechert & Bishop 1990; Landis et al. 2000; McIntyre 2000; Öberg 2007) and on islands (e.g., Schoener & Spiller 2006), and it is evident that both natural and human disturbances strongly affect spider abundance and richness. Spiders are also affected by changes in habitat structure including changes to plant richness, architecture, and plant density (Wise 1993). Shochat et al. (2004) found that although spider abundance increased in disturbed areas, spider diversity decreased. They related these changes to the increased abundance of Lycosidae and Linyphiidae individuals in more disturbed and highly productive habitats, contrasting with the drastic decreases in abundance of Clubonidae and Oxyopidae, and thus suggest that rarer species are more susceptible to habitat disturbance. Because spiders are abundant and dominant predators, Shochat et al. (2004) predicted that spiders should be strongly influenced by habitat fragmentation and other anthropogenic changes such as urbanization. In support, a study by Magura et al. (2010b) found that spider diversity increased in disturbed areas due to increased alteration of habitat, leading to a wider variety of niches and, consequently, spider diversity. In contrast, Alaruikka et al. (2002) investigated changes in spider abundance and richness along an urban to rural gradient in Finland, but did not find any significant differences. Nonetheless, potential losses of spider diversity and changes in species composition with urbanization may have practical

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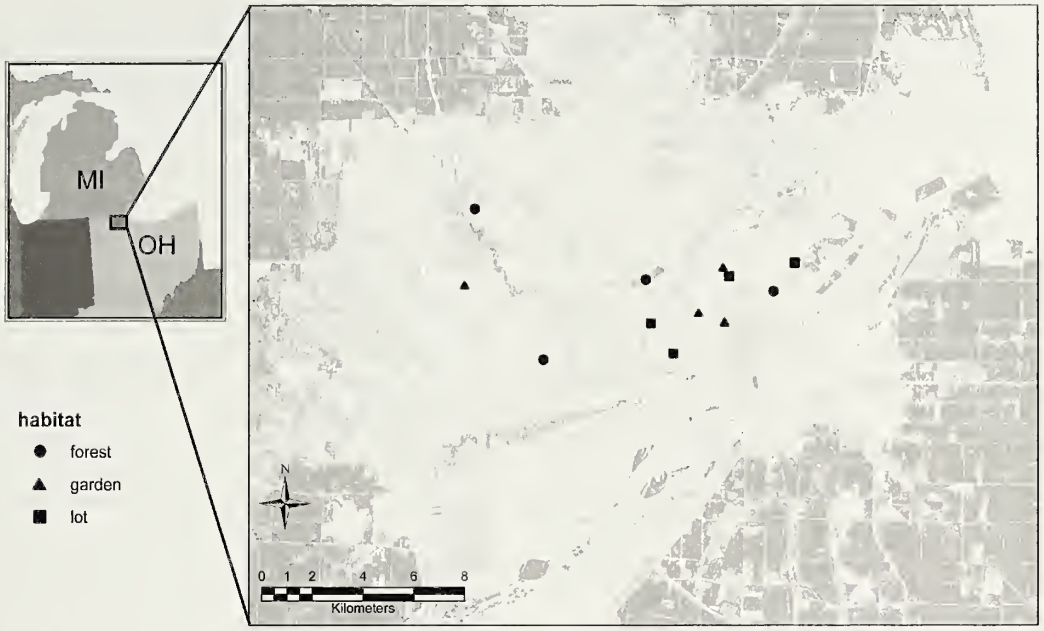

Figure 1.—Location of urban study sites in Toledo, Ohio. Sites sampled included natural forests (F), community gardens (G) and vacant lots (V).

importance in urban habitats because spiders are natural predators and valuable as naturally occurring pest control agents (Marc et al. 1999).

We examined spider aetivity-density (a measure of both abundance within a habitat and degree of movement), species richness and species composition in three different habitat types in an urban area. Specifically, we examined spider communities collected from community gardens, vacant lots and small forest fragments across a four-month period to examine 1) differences in richness, activity-density, and composition of ground-dwelling spiders in different urban habitat types; 2) differences in richness, activity-density, and composition of ground-dwelling spiders in different sample months and 3) the specific habitat characteristics that correlate with changes in spider communities in urban habitats. Based on previous studies of spiders in urban and agricultural habitats, we hypothesized that gardens and lots would have higher spider activity-density and lower richness than forest fragments.

METHODS

Study sites.—We conducted our study in Toledo, Ohio (41°39′56″N, 83°34″31′W), a city with a population of 295,614 that covers roughly 208 km^2 (United States Census Bureau 2006–2008). We sampled spiders in three urban habitat types: community gardens (gardens), vacant lots (lots), and forest fragments (forests). We established four replicate sites of each habitat type distributed throughout the city for a total of 12 study sites (Fig. 1). Study sites were located between 0.5–13.1 km apart, with no significant difference in the mean distance between gardens (5.8 ± 1.9 km (SE)), lots (3.9 ± 0.8 km) and forests (7.7 ± 1.1 km) ($F_{2,15}$ = 2.0, P = 0.18). Sites were chosen to be as similar as possible in terms of the surrounding landscape condition and the habitat extent (e.g. patch size). The forest fragments were located within Toledo City Parks, and ranged from 30,750–85,000 m^2. Gardens were all facilitated by an urban gardening outreach program, Toledo Grows of the Toledo Botanical Garden, had been in vegetable production for at least five years prior to the study, and were between 420–2688 m^2. The vacant lots ranged in size from 1299–8262 m^2, were all managed (and owned) by the city of Toledo and were vacant for at least nine years prior to the study. Vacant lots are a significant habitat type in Toledo, with more than 1000 vacant lots distributed throughout the city (Uno et al. 2010).

Spider sampling and identification.—We sampled spiders with pitfall traps. At each site, we placed 6 pitfall traps in a 5 × 10 m grid with traps placed 5 m apart. The traps consisted of two 473mL (16 oz.) cups, 11.4 cm in diameter and 7.6 cm in depth. One cup was a placeholder put just below ground level and sealed when not in use. Inside these cups we placed a second cup, flush with the surface to capture ground-dwelling arthropods. During trap days, we placed 200 ml of a saturated saline solution with a small amount of detergent to break surface tension in the cups. We then placed green plastic plates held up with small nails over the traps (~ 8 cm above ground level) to exclude rainwater. Every month from May to August, traps were left open for three days. Trap dates during 2007 were as follows: May 6–10, June 4–7, July 2–5, and July 30–August 2. Within each site, we placed traps toward the center of the habitat patch to limit edge effects. After three days, we retrieved the traps, rinsed the contents with deionized water to remove the salt solution and stored arthropods in 70% ethyl alcohol. During non-trap days, traps remained in the exact same locations within the soil, and we covered all traps with Tupperware lids when not in use.

We first sorted arthropods in order to separate the spiders from the collection. Then we identified spiders to family using Ubick et al. (2005) and Bradley (2004). We then sorted all adult spiders to genus where possible, and, subsequently, to

morphospecies. Identification to at least the family level allows for comparison between different habitats (Shochat et al. 2004). We recorded sex for each spider and only included adult spiders in data analyses. We stored specimens in 70% ethyl alcohol. Specimens are now stored at the Environmental Studies Department at the University of California, Santa Cruz.

Habitat characteristics.—We quantified 24 site characteristics of the urban habitats surrounding the pitfall traps at three spatial scales. We first measured the extent of habitat patch (e.g., contiguous garden, lot or forest habitat) surrounding pitfall traps. We then established 100 × 100 m plots centered on pitfall traps within which we quantified percent area covered with a) concrete, b) buildings, c) bare ground, d) grass or herbs and e) shrubs. Within 100 × 100 m plots, we also counted the number of trees >30 cm circumference at breast height (cbh). We also established 20 × 20 m plots centered on the spider sampling area. In the 20 × 20 m area we sampled canopy cover with a concave vertical densiometer at each corner and the center of each plot. We also counted and identified all trees >30 cm cbh, measured tree circumference at 1.37 m above the ground, and estimated tree height. We identified and measured height and circumference (at 1 cm above ground) of all tree seedlings and shrubs < 2 m tall and calculated total woody plant richness per site. Finally, within the 20 × 20 m plots, we randomly placed four 1 × 1 m plots to examine herbaceous vegetation and ground cover. Within each 1 × 1 m plot, we estimated percent cover of a) bare ground, b) grasses, c) forbs and herbs, d) rocks/wood panels, e) leaf litter and f) fallen branches. We recorded a) height of the tallest non-woody vegetation, b) number of forbs and herbs and c) richness of forbs, herbs, and grasses.

Data analysis.—To examine spider richness, we plotted species accumulation curves for each habitat type and each sample date with EstimateS (Colwell 2005) and determined significant differences between habitat types and sample dates by comparing overlap in 95% confidence intervals (CIs). We plotted curves for males and females separately due to use of morphospecies and common sexual dimorphism for spiders. We assessed spider activity-density data and treated each site on each date as a sample, summing across the 6 pitfall traps. We used sample-based rarefaction curves standardized to the number of individuals to compare species richness (Gotelli & Colwell 2001).

We compared spider activity-density between habitats and between sampling dates using a repeated measures analysis of variance (ANOVA). We summed activity-density across all pitfall traps in a site and then examined activity-density of all spiders, of males or of females as the dependent variable and sampling date and habitat type as main factors. We natural log (+1) transformed activity-density data for all and male spiders to meet conditions of normality. We used Tukey's tests to distinguish significant differences between pairs of habitat types and between sample dates. We also compared the activity-density of the five most common families encountered with multivariate ANOVA with number of spiders of each family captured as the dependent variables and habitat type, date, and gender as the main factors. We conducted all activity-density analyses with SPSS v. 17.

We compared family and morphospecies composition of spiders in the three urban habitats and four sample dates with three methods. First, we used non-metric multi-dimensional scaling (NMDS) and analysis of similarities (ANOSIM) to visually and statistically compare composition of spiders. We considered each site as a replicate, summed all occurrences of each species over four sample months, and compared similarity with the Bray-Curtis similarity index. ANOSIM produces a global P-value to indicate any differences in composition and also reports pair-wise comparisons between particular sites. Third, we used a non-parametric MANOVA (NPMANOVA) to compare the relative differences in family and morphospecies composition in sites of the same habitat type or sampled on the same date (e.g., spread of the points). All composition analyses were conducted with PAST (Hämmer et al. 2001).

We examined differences in site characteristics measured in each habitat type and then examined which characteristics best correlated with changes in spider communities. To examine differences in site characteristics in the three different habitats, we used a multivariate ANOVA with each of the 24 site variables as dependent variables and habitat type as the main factor. To examine relationships between the site characteristics and spider communities, we first used a Principal Components Analysis (PCA) to reduce the 24 possible explanatory variables into principal components. Then we correlated PCA axis 1 and axis 2 with individual vegetation variables with Pearson's correlations to determine which variables were significantly explained by the two principal components, and thus which biological factors were explained by each component. Then, we used multivariate regressions to examine whether PCA axes 1 and 2 and other remaining variables (e.g., those not significantly correlated with PCA axis 1 or 2) predicted total observed spider richness, or NMDS dimensions 1 and 2 for spider family and morphospecies composition. Variables representing pereent ground cover at the 100 × 100 m and 1 × 1 m scale were arcsine-root transformed; counts of trees, shrubs and herbs were log (ln+1) transformed and habitat size was square-root transformed to meet conditions of normality before any analysis. All vegetation, PCA, and regression analyses were conducted with SPSS v. 17.0.

RESULTS

Spider activity-density.—We collected 547 adult spiders from pitfall traps from 19 families across all habitats. Overall, more male (328) than female (219) spiders were collected. On average, across the summer, spider activity-density was higher in lots than in forests (Table 1). There were also differences in activity-density of female and male spiders with habitat type (Table 1). Female spider activity-density was higher in lots than in gardens, and higher in gardens than in forests. Male spider activity density was higher in lots than in forests. Spider activity-density was relatively constant over the summer, with 8.9 ± 1.3 individuals per site in May, 10.0 ± 1.5 individuals in June, 11.2 ± 2.3 individuals in July and 15.5 ± 2.7 individuals in August (ANOVA, $F_{3,\ 27} = 2.2$, $P = 0.10$). Further, there was no significant interaction between habitat type and sampling date (ANOVA, $F_{6,\ 27} = 1.8$, $P = 0.15$).

The most common families encountered were ground-foraging families: Lycosidae (34.37% of individuals), Corinnidae (8.78%), Liocranidae (8.23%), Cybaeidae (7.68%) and

Table 1.—Activity density of spiders in three urban habitats in forests, gardens and vacant lots in Toledo, Ohio. Values for forests, gardens and lots show mean ± standard error, and different superscript letters designate significant differences between habitats (Tukey's test, $P < 0.05$). Statistical results are from univariate ANOVA tests.

	Garden	Lot	Forest	$F_{2,9}$	P
All spiders	$39.75 \pm 5.67^{a,b}$	70.75 ± 4.49^{a}	26.25 ± 6.37^{b}	9.4	0.006
Male spiders	$21.50 \pm 2.90^{a,b}$	43.00 ± 6.61^{a}	17.50 ± 5.30^{b}	4.8	0.039
Female spiders	18.25 ± 3.12^{b}	27.75 ± 2.46^{a}	8.75 ± 2.18^{c}	17.6	0.001

Dictynidae (7.31%). Activity-density of different families differed with habitat type (ANOVA, $F_{10,138} = 11.1$, $P < 0.001$; Fig. 3) and gender (ANOVA, $F_{5,68} = 4.4$, $P = 0.002$). Speeifically, aetivity-density of Corinnidae was higher in forests than in lots (ANOVA, $F_{2,72} = 4.2$, $P= 0.014$,), activity-density of Dictynidae was higher in lots than in forests (ANOVA, $F_{2,72} = 39.9$, $P < 0.001$) and than in gardens (ANOVA, $F_{2,72} = 39.9$, $P < 0.001$), and Lycosidae were encountered at least twice as often in lots and in gardens as in forests (ANOVA, $F_{2,72} = 29.9$, $P < 0.001$). Activity-density of males was higher for Corinnidae (ANOVA, $F_{1,72} = 6.3$, $P = 0.011$) and Dictynidae (ANOVA, $F_{1,72} = 9.6$, $P = 0.003$). There were significant interactions between habitat type and gender (ANOVA, $F_{10,138} = 2.7$, $P = 0.005$).

Spider richness and composition.—Overall we collected 62 female morphospecies and 52 male morphospecies of spiders. According to species accumulation curves and 95% CI for female and male spiders, there were no significant differences in richness in the three habitat types; however, for both females and males, richness tended to be highest in vacant lots and lowest in forests (Fig. 3a, b). None of the accumulation curves reached asymptotes, indicating that spiders were not completely sampled in any habitat.

According to NMDS and ANOSIM, composition of spider families differed with habitat type (ANOSIM, $P = 0.002$, Fig. 4a). Spider families found in forests differed from those in lots (ANOSIM, $P = 0.029$) and tended to differ from those in gardens (ANOSIM, $P = 0.06$). Similarly, at the level of morphospeeies, spider composition differed with habitat type both for females (ANOSIM, $P = 0.002$, Fig. 3b) and males (ANOSIM, $P = 0.008$, Fig. 4c). Female morphospecies composition differed in forests and gardens (ANOSIM, $P = 0.029$), and male morphospecies composition tended to differ in forests and lots (ANOSIM, $P = 0.057$). Spider family composition was more dissimilar in individual forest sites (e.g., composition of forest spiders was more widely distributed) than in gardens (ANOSIM, $P = 0.06$) or in lots (ANOSIM, $P = 0.031$) (NPMANOVA, $F = 2.3$, $P = 0.005$). Female morphospecies composition was more dissimilar in forest sites than in lots (NPMANOVA, $P = 0.029$) and more dissimilar in forest sites than in gardens (NPMANOVA, $P = 0.025$) (NPMANOVA, $F = 1.8$, $P = 0.002$). Male morphospecies composition tended to be more dissimilar in forest sites than in lots (NPMANOVA, $F = 2.3$, $P = 0.005$).

Habitat characteristics and spider richness and composition.—Several site characteristics differed with habitat (MANOVA, $F_{4,18} = 9.6$, $P = 0.004$, Table S1 [Supplemental materials are available online at http://www.bioone.org/doi/suppl/10.1636/P12-44]). Forests were larger, had more and larger shrubs and trees, higher richness of woody plants, more canopy cover, and more fallen branches (Table S1). Lots and gardens were more surrounded by buildings and concrete (Table S1). Vacant lots had taller non-woody vegetation than forests, and more grass cover, and gardens had more rock and wood cover, more forb cover and higher herb richness (Table S1). The PCA predicted a large fraction of the variation in habitat characteristics and reduced the site characteristics from 24 to 6. PC1 explained 48.2%, PC2 explained 17.6% and PC1-5 explained 89.5% of the variation in the habitat characteristic data. Sixteen factors correlated with PC1 and four factors correlated with PC2 (Table S2 [Supplemental materials are available online at http://www.bioone.org/doi/suppl/10.1636/P12-44]). PC1 positively correlated with amount of concrete, buildings, and grass cover and negatively correlated with % cover of herbs, shrubs,

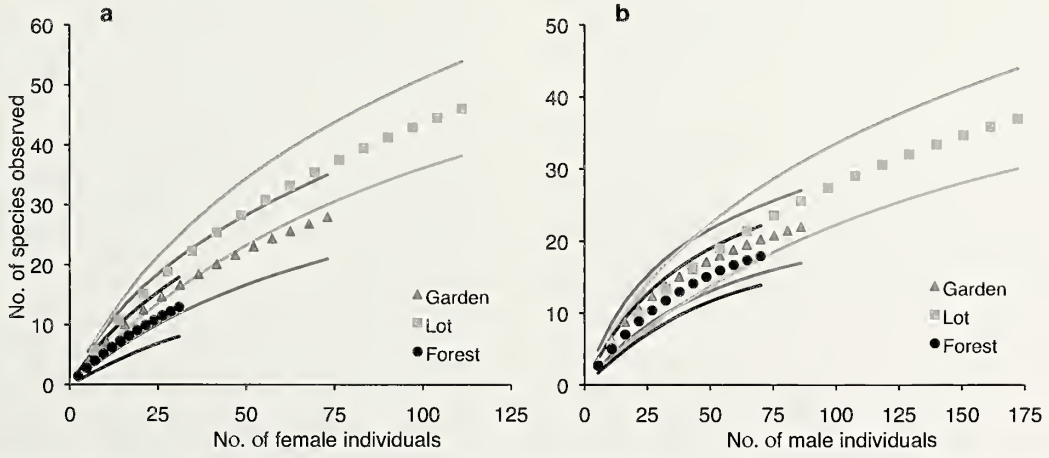

Figure 2.—Species accumulation curves for observed spider species richness for a) females and b) males observed in urban forests, community gardens and vacant lots sampled in Toledo, Ohio. Thin lines show upper and lower 95% confidence intervals for symbols of the same shading.

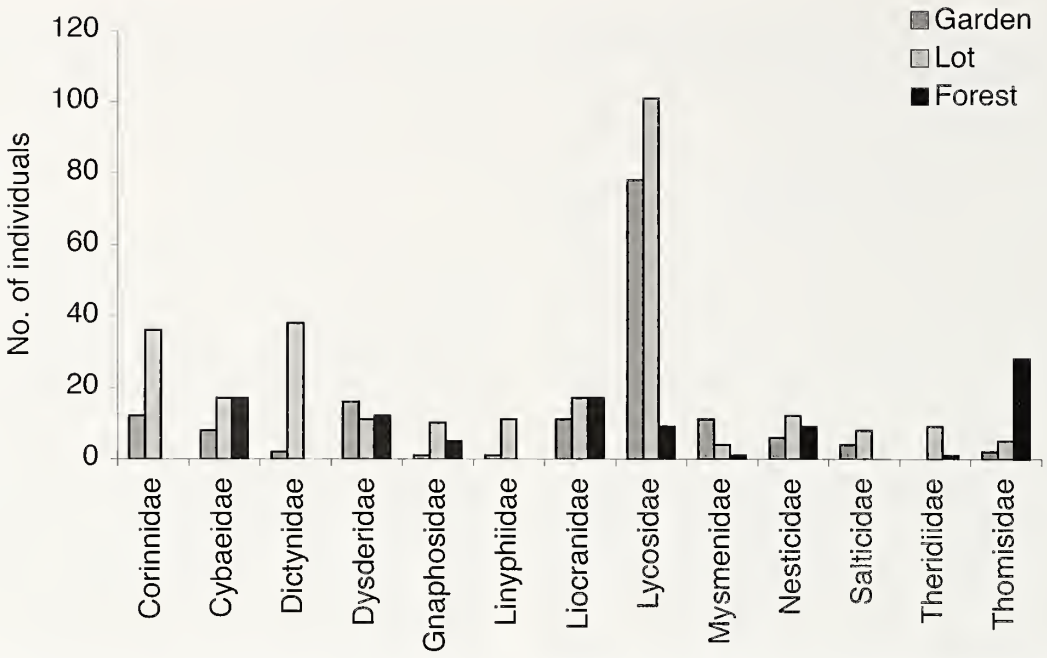

Figure 3.—Rank abundance curves for spider families collected in community gardens, vacant lots, and forest fragments in Toledo, Ohio. All families shown were represented by at least 10 individuals across all habitat types and are arranged alphabetically.

trees, and tree size. Other components (PC3, PC4, PC5) did not correlate with other site characteristics.

Spider composition was not well predicted by the measured site characteristics; richness correlated with some habitat changes. PC1, PC2 and four remaining vegetation factors explained >70% of the variation in composition of different spider groups, yet were not significant predictors of female morphospecies composition (NMDS 1, $F_{6,11} = 2.0$, $P = 0.24$; NMDS 2, $F_{6,11} = 2.9$, $P = 0.13$), male morphospecies composition (NMDS 1, $F_{6,11} = 2.3$, $P = 0.19$; NMDS 2, $F_{6,11} = 3.5$, $P = 0.09$), or spider family composition (NMDS 1, $F_{6,11} = 1.4$, $P = 0.38$; NMDS 2, $F_{6,11} = 6.2$, $P = 0.032$; spider family composition did not correlate with any individual site characteristics ($P > 0.05$). Site characteristics explained 90.9% of the variation in observed species richness of females (Multivariate regression, $F_{6,11} = 8.4$, $P = 0.017$), and female richness decreased with increased bare ground ($t = -2.7$, $P = 0.043$), but did not correlate with other factors. Site characteristics explained 53.3% of the variation in male spider richness, but were not significantly correlated (Multivariate regression, $F_{6,11} = 1.0$, $P = 0.53$).

DISCUSSION

Spider activity-density differed with habitat but did not significantly vary with sampling date. Overall, the activity-density that we observed for spiders (22.7 spiders per trap per month) was consistent with what others have found in urban and agricultural habitats (between 0.4 and 15.9 spiders per trap per month: Shochat et al. 2004; Dias et al. 2006; Magura et al. 2010b). We collected more spiders in lots than in forests for all, and male spiders and female activity-density was greater in lots than in gardens and greater in gardens than in forests. These results are consistent with other studies that have found greater spider activity-density in more disturbed habitats (Samu et al. 1999; Bolger et al. 2000; Pinkus-Rendón et al. 2006). We did not directly measure habitat disturbance, but forest fragments were relatively undisturbed, whereas the lots experienced mowing, and gardens were tilled, planted, and experienced heavy human activity during the summer. Several characteristics of the sampled habitats may have influenced spider activity-density. For instance, higher prey activity-density may support higher predator activity-density (Bultman & Uetz 1982; Miyashita et al. 1998) and more active foraging of spiders (Bradley 1993). Yet prey activity-density may not be as important in determining activity-density and composition patterns as other habitat characteristics, especially during mid-summer (Bultman & Uetz 1982). Spider prey may be more abundant in areas with high amounts of grass cover (Bolger et al. 2000), and vacant lots had higher grass cover at the smallest scale measured. Spider activity-density, especially of some lycosids, one commonly encountered group, also increases with the amount of thatch (Döbel et al. 1990; Denno et al. 2002). We did not measure thatch cover, but this may be correlated with grass cover, which was higher in vacant lots.

Many factors at both local and landscape scales likely influence spider richness. For example, vegetation complexity can influence spiders by altering temperature, humidity, prey activity-density and richness, and number of prey refuges (Bultman & Uetz 1982; Wise 1993; Samu et al. 1999; Denno et al. 2002). Here, observed richness showed no significant differences between habitats. Spider diversity can differ with agricultural or urban habitat differences (Miyashita et al. 1998; Shochat et al. 2004; McKinney 2008) or along rural to urban gradients (Magura et al. 2010b). However, as in this study, others have found limited or no differences in richness among different urban and agricultural habitats (Alaruikka et al. 2002). McKinney (2008) reported declines in spider diversity with increasing amounts of impervious surface and declines in vegetation complexity; yet for some situations, spider richness was not affected or even increased with

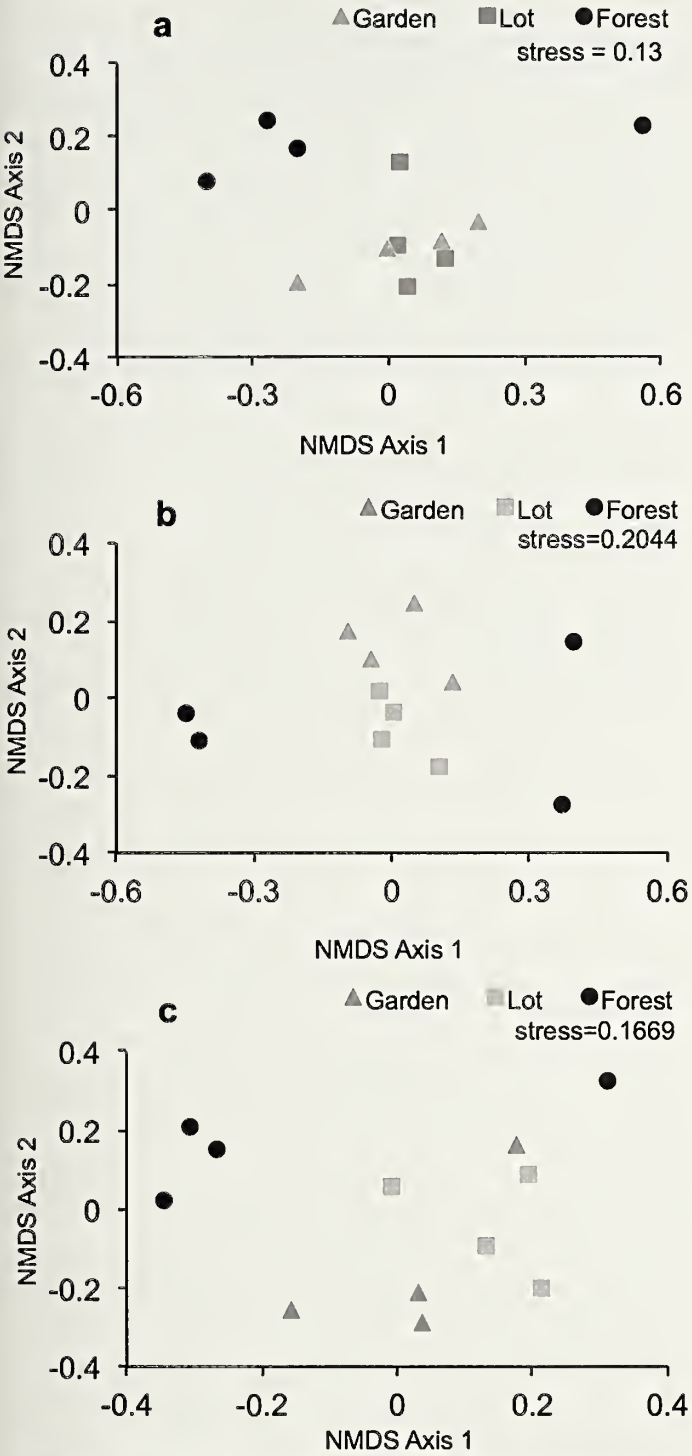

Figure 4.—Non-metric multi-dimensional scaling analysis of spiders collected in urban habitats in Toledo, Ohio showing a) family composition and b) morphospecies composition of females and c) morphospecies composition of males in different habitat types.

urbanization. Similarly, Magura et al. (2010b) did not find differences in richness of ground-dwelling spiders in urban, suburban and rural habitats. Further, Clough et al. (2005) and Pinkus-Rendón et al. (2006) found similar spider richness in organic vs. conventional farms, and Pinkus-Rendón et al. (2006) also found no clear diversity gradient in coffee farms managed with a more or less complex shade tree canopy. Thus our results, showing minor differences in spider richness with changes in habitat are not unusual.

Spider composition also differed with habitat type at the level of family and for female and male morphospecies. Composition was generally more similar in the two open habitats: lots and gardens. Since the vegetation differed with habitat type, it is not surprising that the community differed in different habitats. In fact, spider species composition differs in disturbed and undisturbed habitats (Bolger et al. 2000; Bonte et al. 2002; Öberg 2007), or in urban forests and heaths differing in fragment size (Gibb & Hochuli 2002). Further, different forest types, including a highly disturbed clear-cut forest, differ dramatically in terms of species composition (e.g., Pearce et al. 2004). However, we did not find strong correlations between vegetation variables examined or changes in spider richness and composition, indicating that other factors may be more important for spider communities. For example, landscape factors, such as habitat edges, landscape heterogeneity and habitat fragment size may influence spiders in agricultural landscapes (Bolger et al. 2000; Clough et al. 2005; Drapela et al. 2008). Spider diversity may vary with distance to habitat edges, and both landscape heterogeneity and location of the fields within the landscape may affect diversity and activity-density of spiders (Clough et al. 2005). Both habitat fragment size and age may also influence spider richness, especially for spiders with larger body size (Miyashita et al. 1998; Bolger et al. 2000). We did not examine the landscape surrounding our study sites. Thus, possibly the landscape surrounding our study sites differs, potentially masking effects of local scale vegetation or site differences on spider diversity.

Spiders tended to be more abundant and species-rich in lots than in the other habitat types, and composition strongly varied in the different urban green space habitats. One aim of this study was to examine the potential of different urban green habitats to conserve biodiversity, thus a comparison to nearby natural areas is important. Bradley and Hickman (2009) recently examined spider communities in several habitats within the Glen Helen Nature Preserve in Greene County (central Ohio). They used several methods, including pitfalls, to sample spiders, making direct comparisons difficult. Nonetheless, they sampled upland forests (77 species collected) and old fields (41 species found). Overall, 26% of the species they captured were with pitfall traps, but they did not report exact values for each habitat type. We collected 13 female and 18 male species in forests, and 46 female and 37 male species in lots; thus, values at least for the open habitats are relatively comparable with natural habitats in the region. In sum, vacant lots support slightly higher richness and greater spider activity-density than other urban habitats examined, and appear comparable to spider richness from nearby natural locations. Because spider composition differs with urban green space habitat, maintaining a variety of habitat types may be most beneficial for spider conservation in urban landscapes.

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LITERATURE CITED

Alaruikka, D., D.J. Kotze, K. Matvcinen & J. Niemelä. 2002. Carabid beetle and spider assemblages along a forested urban-rural gradient in southern Finland. Journal of Insect Conservation 6:195–206.

Bolger, D.T., A. Suarez, K. Crooks, S. Morrison & T. Case. 2000. Arthropods in urban habitat fragments in southern California: Area, age, and edge effects. Ecological Applications 10:1230–1248.

Bonte, D., L. Baert & J. Maelfait. 2002. Spider assemblage structure and stability in a heterogeneous coastal dune system (Belgium). Journal of Arachnology 30:331–343.

Bradley, R.A. 1993. The influence of prey availability and habitat on activity patterns and abundance of *Argiope keyserlingi* (Araneae: Araneidae). Journal of Arachnology 21:91–106.

Bradley, R.A. 2004. In Ohio's Backyard: Spiders. Ohio Biological Survey Backyard Series No. 4. Columbus, Ohio.

Bradley, R.A. & W.L. Hickman. 2009. Spiders (Araneae) of the Glen Helen Nature Preserve, Greene County, OH. Ohio Journal of Science 109:3–14.

Bultman, T.L. & G.W. Uetz. 1982. Abundance and community structure of forest floor spiders following litter manipulation. Oecologia 55:34–41.

Cárdenas, A.M. & C.M. Buddle. 2009. Introduced and native ground beetle assemblages (Coleoptera: Carabidae) along a successional gradient in an urban landscape. Journal of Inseet Conservation 13:151–163.

Carpaneto, G.M., A. Mazziotta & E. Piatella. 2005. Changes in food resources and conservation of scarab beetles: from sheep to dog dung in a green urban area of Rome (Coleoptera, Scarabaeoidea). Biological Conservation 123:547–556.

Christie, F.J. & D.F. Hochuli. 2009. Responses of wasp communities to urbanization: effects on community resilience and species diversity. Journal of Insect Conservation 13:213–221.

Clough, Y., A. Kruess, D. Kleijn & T. Tscharntke. 2005. Spider diversity in cereal fields: eomparing factors and local, landscape, and regional scales. Journal of Biogeography 32:2007–2014.

Colwell, R.K. 2005. EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.0.0. Online at http://viceroy.eeb.uconn.edu/estimates.

Dias, S.D., A. Brescovit, E. Couto & C. Martins. 2006. Species riehness and seasonality of spiders (Arachnida: Araneae) in an urban Atlantic Forest fragment in Northeastern Brazil. Urban Ecosystems 9:323–335.

Denno, R.F., C. Gratton, M.A. Peterson, G.A. Langellotto, D.L. Finke & A.F. Huberty. 2002. Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. Ecology 83:1443–1458.

Döbel, H.G., R.F. Denno & J.A. Coddington. 1990. Spider (Araneae) community structure in an intertidal salt marsh: effects of vegetation structure and tidal flooding. Environmental Entomology 19:1356–1370.

Drapela, T., D. Moser, J.G. Zaller & T. Frank. 2008. Spider assemblages in winter oilseed rape affected by landscape and site factors. Ecography 31:254–262.

Elek, Z. & G.L. Lövei. 2007. Patterns in ground beetle (Coleoptera: Carabidae) assemblages along an urbanization gradient in Denmark. Acta Oecologica 32:104–111.

Fattorini, S. 2011. Insect extinction by urbanization: A long term study in Rome. Biological Conservation 144:370–375.

Gibb, H. & D. Hochuli. 2002. Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biological Conservation 106:91–100.

Gotelli, N.J. & R.K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379–391.

Hämmer, Ø., D.A.T. Harper & P.D. Ryan. 2001. Past: paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4:1–9.

Hornung, E., B. Tóthmérész, T. Magura & F. Vilisics. 2007. Changes of isopod assemblages along an urban–suburban–rural gradient in Hungary. European Journal of Soil Biology 44:158–165.

Landis, D.A., S. Wratten & G. Gurr. 2000. Habitat management to eonserve natural enemies of arthropod pests in agriculture. Annual Review of Entomology 45:175–201.

Magura, T., G.L. Lövei & B. Tóthmérész. 2010a. Does urbanization decrease diversity in ground beetle (Carabidae) assemblages Global Ecology and Biogeography, 19:16–26.

Magura, T., R. Horváth & B. Tóthmérész. 2010b. Effect of urbanization on ground dwelling spiders in forest patches, in Hungary. Landscape Ecology 25:621–629.

Marc, P., A. Canard & F. Ysnel. 1999. Spiders (Araneae) useful for pest limitation and bioindication. Agriculture, Ecosystems & Environment 74:229–273.

Markovchick-Nicholls, L., H. Regan, D. Deutschman, A. Widyanata, B. Martin, L. Noreke & T. Hunt. 2008. Relationships between human disturbance and wildlife land use in urban habitat fragments. Conservation Biology 22:99–109.

McIntyre, N.E. 2000. Ecology of urban arthropods: a review and a call to action. Annals of the Entomological Society of America 93:825–835.

McKinney, M.L. 2002. Urbanization, biodiversity and conservation. Bioscience 52:883–890.

McKinney, M.L. 2008. Effects of urbanization on species richness: A review of plants and animals. Urban Ecosystems 11:161–176.

Miller, J.R. & R.J. Hobbs. 2002. Conservation where people live and work. Conservation Biology 16:330–337.

Miyashita, T., A. Shinkai & T. Chida. 1998. The effects of forest fragmentation on web spider communities in urban areas. Biological Conservation 86:357–364.

Öberg, S. 2007. Diversity of spiders after spring sowing – influence of farming system and habitat type. Journal of Applied Entomology 131:524–531.

Paeheco, R. & H.L. Vasconcelos. 2007. Invertebrate conservation in urban areas: Ants in the Brazilian Cerrado. Landscape and Urban Planning 81:193–199.

Pearce, J.L., L.A. Venier, G. Eccles, J. Pedlar & D. McKenney. 2004. Influence of habitat and microhabitat on epigeal spider (Aranae) assemblages in four stand types. Biodiversity and Conservation 13:1305–1334.

Pinkus-Rendón, M.A., G. Ibarra-Núñez, V. Parra-Table & J.A. García-Ballinas. 2006. Spider diversity in coffee plantations with different management in Southeast Mexico. Journal of Arachnology 34:104–112.

Rango, J.J. 2005. Arthropod communities on creosote bush (*Larrea tridentate*) in desert patches of varying degrees of urbanization. Biodiversity and Conservation 14:2185–2206.

Riechert, S.E. & L. Bishop. 1990. Prey eontrol by an assemblage of generalist predators: Spiders in garden test systems. Ecology 71:1441–1450.

Sadler, J.P., E.C. Small, H. Fiszpan, M.G. Telfer & J. Niemelä. 2006. Investigating environmental variation and landscape characteristics of an urban-rural gradient using woodland carabid assemblages. Journal of Biogeography 33:1126–1138.

Samu, F., K. Sunderland & C. Szinetár. 1999. Scale-dependent dispersal and distribution patterns of spiders in agricultural systems: A review. Journal of Arachnology 27:325–332.

Schoener, T.W. & D.A. Spiller. 2006. Nonsynchronous recovery of community charaeteristics in island spiders after a catastrophic hurricane. Proceedings of the National Academy of Sciences of the United States of America 103:2220–2225.

Shochat, E., W. Stefanov, M. Whitehouse & S. Faeth. 2004. Urbanization and spider diversity: Influences of human modification of habitat structure and productivity. Ecological Applications 14:268–280.

Shoehat, E., P.S. Warren, S.H. Faeth, N.E. McIntyre & D. Hope. 2006. From patterns to emerging processes in mechanistic urban ecology. Trends in Ecology & Evolution 21:186–191.

Smith, R.M., P.H. Warren, K. Thompson & K.J. Gaston. 2006. Urban domestic gardens (VI): environmental correlates of invertebrate species richness. Biodiversity and Conservation 15:2415–2438.

Thompson, B. & S. McLachlan. 2007. The effects of urbanization on ant communities and myrmecochory in Manitoba, Canada. Urban Ecosystems 10:43–52.

Tonietto, R., J. Fant, J. Ascher, K. Ellis & D. Larkin. 2011. A comparison of bee communities of Chicago green roofs, parks, and prairies. Landscape and Urban Planning 103:102–108.

Tóthmérész, B., I. Máthé, E. Balázs & T. Magura. 2011. Responses of carabid beetles to urbanization in Transylvania (Romania). Landscape and Urban Planning 101:330–337.

Turner, W.R., T. Nakamura & M. Dinetti. 2004. Global urbanization and the separation of humans from nature. Bioscience 54:585–590.

Ubick, D., P. Paquin, P.E. Cushing, & V. Roth (eds.). 2005. Spiders of North America: an Identification Manual. American Arachnological Society, Poughkeepsie, New York.

United Nations Information Service. 2004. World Urbanization Prospects: UN Report Says World Urban Population of 3 Billion Today Expected to Reach 5 Billion by 2030. United Nations, New York.

United States Census Bureau. 2006–2008. Toledo, OH Fact Sheet. Online at http://factfinder.census.gov/servlet/ Accessed 26 February 2010.

Uno, S., J. Cotton & S.M. Philpott. 2010. Diversity, abundance, and species composition of ants in urban green spaces. Urban Ecosystems 13:425–441.

Varet, M., J. Pétillon & F. Burel. 2011. Comparative responses of spider and carabid beetle assemblages along an urban-rural boundary gradient. Journal of Arachnology 39:236–243.

Vilisics, F., Z. Elek, G.L. Lövei & E. Hornung. 2007. Composition of terrestrial isopod assemblages along an urbanization gradient in Denmark. Pedobiologia 51:45–53.

Wilcove, D.S., D. Rothstein, J. Dubow, A. Phillips & E. Losos. 1998. Quantifying threats to imperiled species in the United States. Bioscience 48:607–615.

Wise, D.H. 1993. Spiders in Ecological Webs. Cambridge University Press, Cambridge, UK.

Yamaguchi, T. 2004. Influence of urbanization on ant distribution in parks of Tokyo and Chiba City, Japan. Ecological Research 19:209–216.

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Diversity and ecology of spider assemblages of a Mediterranean wetland complex

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Abstract. Wetland complexes in Mediterranean deltas play an important ecological role, as they harbor a diverse flora and fauna with numerous specialized species. Intensification and expansion of agricultural land use, as well as increasing withdrawal of water over the past decades, has led to considerable habitat loss in many places. Although studies from temperate Europe have already demonstrated the conservation needs of wetlands, analogous data for the Mediterranean region are very scarce. The present paper analyzes spider assemblages of the Aladjagiola wetland complex and provides ecological descriptions of diversity patterns and assemblage structures. We aim to provide the first ecological descriptions of several species and effective data sets to characterize the ecological status of the wetland habitats investigated. Spiders were collected by pitfall trapping from April to July 2008 in seven habitat types: pseudo-maquis, dry grassland (short growth), dry grassland (long growth), fringes, reed belts, humid grassland and fallow land. Diversity (alpha and functional) and evenness were both found to be lowest in humid habitat types. Community structure was analyzed by non-metric multidimensional scaling. Humid habitat types harbored a distinct species assemblage comprising many hygrophilic species that could clearly be separated from all other habitat types. By means of generalized linear models, habitat preferences of numerous xerophile, hygrophilic and photophilic species could be assessed. Our study demonstrated that especially humid habitat types are worth protecting.

Keywords: Aladjagiola wetland complex, Araneae, east Macedonian-Thracian wetland belt, functional diversity, Greece, Nestos Delta

Mediterranean deltas comprise a broad variety of habitat types (Heeker & Vives 1995). Among them, coastal dunes and lagoons with salt marshes, as well as fresh-water habitats such as dynamic riparian gravel and sand banks, alluvial forests, lakes and adjacent wetlands play an important ecological role, as they harbor a diverse flora and fauna including numerous specialized species (Kremar & Merdic 2007; Buchholz 2009). Most Mediterranean deltas have been heavily impacted by anthropogenic measures (e.g., drainage, water storage, salinization, grazing and pisciculture) and are thus highly endangered (Britton & Crivelli 1993).

The Aladjagiola wetland complex is located in northeast Greece within the Nestos Delta, forming the westernmost part of the east Macedonian and Thracian wetland belt. Although covering a relatively small area (approximately 20 km^2), previous studies have consistently indicated high species richness within numerous taxonomic groups (amphibians and reptiles: Donth 1996; butterflies: Schumann 1996; spiders: Schröder et al. 2011). Despite their ecological relevance, the wetlands of the Aladjagiola have been subjected to a continuous intensification and expansion of agricultural land use over the past decades. Together with an increasing withdrawal of water, this has led to considerable habitat loss in the whole region (Mallinis et al. 2011). Currently, the conversion of land and the alteration in water supply of the Nestos River are an immediate threat, which has led to an increasing desiccation of freshwaters and the adjacent wetland habitat types.

Invertebrates such as spiders are generally suitable early warning organisms and bioindicators. By studying invertebrate communities it is possible to assess the conservation value of certain habitat types, and several authors claim a more prominent consideration for conservation and biodiversity studies (Finch & Niedringhaus 2010). In this context, analyzing assemblages and species-environment relationships can provide valuable data bases for nature conservation policies and habitat management guidelines (Buchholz 2010; Cristofoli et al. 2010). Spiders have proven to be a suitable model group within a broad variety of ecological studies (Buchholz 2010; Schirmel et al. 2012) as they are abundant and species-rich, easy to sample and show distinct spatial and temporal habitat preferences (Entling et al. 2007; Schirmel & Buchholz 2011). To date, ecological analyses of spider assemblages of eastern Mediterranean ecosystems are very scarce, and thus information on ecology and habitat preferences of many spider species is mostly missing.

This paper analyzes spider assemblages of the Aladjagiola wetland complex. Apart from ecological descriptions of diversity patterns and assemblage structures, this work aims to provide effective data sets to characterize the ecological status of the investigated habitat types that could be used within the framework of conservation and both ecological planning and management. Authorities for scientific names appear in Appendix I.

STUDY AREA

Aladjagiola is part of the Nestos Delta and is located in East Macedonia, in northeast Greece, between 41°00′ and 41°02′N, and between 24°40′ and 24°44′E. It comprises an area of approximately 20 km^2 (Mattes & Lienau 1996) (Fig. 1). The northern border of the Nestos Delta directly adjoins the southernmost part of the Rhodope Mountains. The study area is located northeast of the city of Chrysoupolis. The climate is Mediterranean with 600–700 mm annual precipitation and 16° C annual average temperature (Lienau 1989).

Within the study area, dry habitats, mainly represented by patches of dry calcareous grassland within scattered pseudo-maquis formations, as well as fresh water lakes with adjacent

Figure 1.—Location of the Aladjagiola wetland complex in the western part of the Nestos Delta, in northeast Greece.

reed banks and humid meadows, form a diverse habitat mosaic. Habitat heterogeneity is additionally enhanced by diverse small-scale vegetation elements within the agricultural landscape, especially fringes and hedges along irrigation canals and arable fields. The biggest lake, Megali Limni, is thought to be a former lagoon that lost its connection to the sea during the delta developing process. Lakes and ponds in the western part of the study site are of anthropogenic origin as a result of intensive clay and sand mining, while standing water bodies near the Nestos River are assumed to have emerged from former oxbows of the Nestos River (Jerrentrup et al. 1989).

METHODS

Sampling.—Spiders were collected by pitfall trapping from April to July 2008. Pitfall traps measured 9 cm in diameter and were filled with a 4% formalin/detergent solution. The position of each trap (three traps per sampling site) was randomly determined, but minimum distance between traps was 5 m. Traps were emptied fortnightly. The investigations were conducted in seven main habitat types (pseudo-maquis, dry grassland – short growth and long growth, fringes, reed beds, humid grassland, fallow land), each with three replicates, resulting in a total of 21 sampling sites and 63 pitfall traps. For habitat description three environmental parameters were assessed once at the end of May (Table 1). Vegetation structure [cover of herb layer (%)] was estimated in an area of 1 m^2 around each pitfall trap. The three measurements per sampling site were afterwards averaged. According to AG Boden (1994), soil humidity was estimated in the field and categorized into five classes: 1 = dry, 2 = slightly humid, 3 = humid, 4 = very humid and 5 = wet. Shading was estimated as percentage of canopy openness and assigned to five shading classes: 1 = no shading (0–20%), 2 = low shading (20–40%), 3 = moderate shading (40–60%), 4 = high shading (60–80%) and 5 = very high shading (80–100%).

Analysis.—Alpha diversity (number of species, Shannon diversity, Shannon evenness) was expressed as the number of species at each site. Shannon diversity and Shannon evenness were calculated using PAST (Hammer et al. 2001).

Although species richness is usually the simplest and most intuitive measure for diversity within the framework of biodiversity and conservation studies, the use of functional diversity, which integrates information on life-history traits, has grown rapidly in recent years in ecological research (e.g., Violle et al. 2007), since the realization that life-history traits play an important role in diversity (Vandewalle et al. 2010). Functional diversity concepts can provide a useful approach to integrate biodiversity research into the broader context of ecosystem processes and functioning, and recently Schirmel et al. (2012) demonstrated that functional diversity of spiders is more sensitive than alpha diversity and therefore contributes valuable information for conservation.

Three functional diversity indices were calculated using the R environment package FD: functional dispersion (FDis), functional evenness (FEve) and functional divergence (FDiv) (Villéger et al. 2008; Laliberté & Legendre 2010). FDis is a measure of functional richness, which considers species relative abundances by estimating their dispersion in a multidimensional trait space. In the following, we interpret functional dispersion as a measure for functional diversity per se. FEve combines both the evenness of trait distribution and the evenness of species relative abundances. The index is 1 if all species have equal abundance and if all the traits are evenly distributed in trait space, and it declines toward zero with

Table 1.—Environmental characteristics of the sampled habitat types. Explanations – classes for soil humidity (soil.hum): 1 = dry, 2 = slightly humid, 3 = humid, 4 = very humid, 5 = wet; classes of shading (measured as canopy openness): 1 = no shading, 2 = low shading, 3 = moderate shading, 4 = high shading, 5 = very high shading; cov.veg = vegetation cover.

habitat type	no. of sites	soil.hum	shading	cov.veg [%]
pseudo-maquis [PM]	3	2	4	75
dry grassland – short growth [DGs]	3	1	1	70
dry grassland – long growth [DGl]	3	2	2	95
fringes [FR]	3	2	3	80
reed belts [RE]	3	5	2	80
humid grassland [HG]	3	4	2	90
fallow land [FL]	3	2	1	70

Table 2.—Spider diversity of habitat types pseudo-maquis (PM), dry grassland – short growth (DGs), dry grassland – long growth (DGl), fringes (FR), reed belts (RE), humid grassland (HG) and fallow land (FL). Alpha diversity is expressed as number of species (number of species), Shannon-Index and Shannon-Evenness (mean ± SEM). For functional diversity, functional dispersion (FDis), functional evenness (FEve) and functional divergence (FDiv) were calculated (mean ± SEM). Differences among habitat types were tested using one-way ANOVA (significance levels: *** $P < 0.001$, ** $P > 0.01$, n.s. = not significant). Pairwise comparisons were done using the Holm-Sidak test, and different letters indicate significant differences between groups at $P < 0.05$.

	habitat types							
	PM	DGs	DGl	FR	RE	HG	FL	*F*
alpha diversity								
no. species	26 ± 3	42 ± 3	40 ± 4	43 ± 2	34 ± 9	40 ± 11	24 ± 2	$1.9^{n.s.}$
Shannon	2.59 ± 0.20^{a}	3.22 ± 0.03^{b}	3.02 ± 0.10^{b}	$2.84 \pm 0.19^{a, b, d}$	2.11 ± 0.18^{c}	2.63 ± 0.15^{d}	$2.56 \pm 0.06^{a, b, d}$	6.8***
Evenness	0.51 ± 0.06^{a}	0.61 ± 0.04^{a}	0.52 ± 0.05^{a}	$0.42 \pm 0.07^{a, b}$	0.26 ± 0.02^{b}	$0.40 \pm 0.08^{a, b}$	0.54 ± 0.03^{a}	4.6**
functional diversity								
FDis	0.38 ± 0.01^{a}	0.36 ± 0.01^{a}	0.38 ± 0.01^{a}	0.34 ± 0.05^{a}	0.26 ± 0.03^{b}	0.24 ± 0.01^{b}	0.40 ± 0.02^{a}	7.1***
FEve	0.71 ± 0.03^{a}	0.71 ± 0.02^{a}	0.69 ± 0.01^{a}	0.71 ± 0.02^{a}	0.59 ± 0.04^{b}	0.60 ± 0.01^{b}	0.72 ± 0.03^{a}	5.2**
FDiv	0.84 ± 0.01	0.79 ± 0.01	0.83 ± 0.03	0.90 ± 0.02	0.89 ± 0.03	0.86 ± 0.03	0.85 ± 0.04	$1.8^{n.s.}$

increasing unevenness in either aspect. Lastly, FDiv expresses the distance of the most abundant species from the centroid of the assemblage in trait space. FDiv is high when the most abundant species have extreme trait values. It ean be interpreted as a measure of variance (Laliberté & Legendre 2010).

To calculate functional diversity, spiders were first assigned to life history trait categories with the help of literature data (Appendix I). The following traits were analyzed: body size, hunting mode and ballooning. Hunting and ballooning were coded eategorically aecording to Cardoso et al. (2011) (ambush hunters, ground hunters, other hunters, orb web, sensing web, sheet web, space web, specialists) and Bell et al. (2005) (ballooning uncommon = genus not listed as ballooners in Bell et al. 2005, less common = genus listed, common = species listed). For body size (total body length), metric data (mm) were taken for females from Nentwig et al. (2013).

For multivariate analyses, only dominant species occurring with frequencies of more than 3.1% per site were taken from the dataset of Schröder et al. (2011). Omitting rare species is an appropriate method to reduce statistical noise in the data set without losing much information. In order to analyze spider species assemblages, a non-metric multidimensional scaling (NMDS) using VEGAN and MASS packages was applied. Prior to the analyses, relative abundances of each species were square root transformed. The NMDS was based on the Bray-Curtis dissimilarity matrix of spiders. In search of a stable solution, a maximum of 100 random starts was used. After seven tries, two convergent solutions were found for a three -dimensional model. A permutational multivariate analysis of variance (MANOVA based on 10,000 permutations) was performed to assess the impact of habitat type and of soil humidity (as an analogue for habitat humidity) on species abundance distribution and assemblage separation.

Poisson generalized linear models (GLM) were applied to test the effects of environmental constraints (predictor variables: soil humidity, shading, vegetation cover) on species that occurred with more than nine individuals. To compensate for overdispersion, standard errors were corrected using a quasi-Poisson model. The residual deviance was used as a goodness-of-fit measure by calculating the pseudo R^2 (Zuur et al. 2009).

All statistical analyses were performed with R 3.0.1 (R Core Team 2013).

RESULTS

Significant differences among habitat types could be detected for Shannon diversity and evenness (ANOVA, $F = 6.8$, $P = 0.001$; $F = 4.6$, $P = 0.007$), although differences in species numbers were not significant (Table 2). Species assemblages of reed belts were less diverse (Shannon = 2.11) than those of all other habitat types. Accordingly, evenness was lowest in reed belts (0.26). Functional diversity also differed significantly among habitat types (Table 2). Functional dispersion and functional evenness were lowest in humid habitat types (FDis = 0.26 and 0.24 for reed belts and humid grassland, respectively, ANOVA, $F = 7.1$, $P = 0.001$; FEve = 0.59 and 0.60, ANOVA, $F = 5.2$, $P = 0.004$). Higher values were calculated for dry habitat types.

In total, 43 species out of 2,208 individuals were submitted to a multivariate analysis. The stress value for a three-dimensional NMDS was 7.92. The scaling plot illustrated two distant habitat groups comprising clearly distinct spider species assemblages (Fig. 2). Humid habitat types (reed, humid grassland) (on the right) were separated from more or less dry habitats on the left. Most abundant in humid habitat types were several lycosid species such as *Arctosa leopardus*, *A. tbilisiensis*, *Aulonia kratochvili*, *Pardosa paludicola*, *P. prativaga*, *P. vittata*, *Pirata latitans* and *Trochosa ruricola* as well as *Oedothorax apicatus*. Dry habitats were separated from pseudo-maquis, where *Brachythele denieri*, *Harpactea babori* and *Scytodes thoracica* were typical species. Dry grassland and fallow land sites harbored a similar species assemblage comprising numerous gnaphosid and salticid species; e.g., *Callilepis cretica*, *Gnaphosa lucifuga*, *Nomisia exornata*, *N. ripariensis*, *Pellenes diagonalis*, *P. nigrociliatus*, *Phlegra fasciata*, *Trachyzelotes barbatus*, *T. lyonneti* and *Zelotes tenuis*.

Soil humdity contributed significantly to species grouping, as indicated by the permutational multivariate analysis of variance ($F = 8.1$, $P < 0.001$, $R^2 = 0.29$, 10,000 permutations). Accordingly, generalized linear models showed that most species responded significantly to soil humidity (Table 3). Activity densities of wetland species such as *Arctosa leopardus*,

Figure 2.—NMDS plot based on spider densities (stress = 7.92, three dimensions). Habitat type significantly affected compositional differences of assemblages (permutational multivariate analysis of variance, $F = 3.3$, $P < 0.001$, $R^2 = 0.69$, 10,000 permutations). Abbreviations—sites: PM1–3 = pseudo-maquis, DGs1–3 = dry grassland, short growth, DGl1–3 = dry grassland, long growth, FR1–3 = fringes, RE1–3 = reed beds, HG1–3 = humid grassland, FL1–3 = fallow land; —species: Alo.alb = *Alopecosa albofasciata*, Arc.leo = *Arctosa leopardus*, Arc.tbi = *Arctosa tbilisiensis*, Aul.kra = *Aulonia kratochvili*, Bra.den = *Brachythele denieri*, Cal.cre = *Callilepis cretica*, Dic.aru = *Dictyna arundinacea*, Dra.pra = *Drassyllus praeficus*, Gna.luc = *Gnaphosa lucifuga*, Hap.sig = *Haplodrassus signifer*, Har.bab = *Harpactea babori*, Hog.rad = *Hogna radiata*, Lio.str = *Liocranoeca striata*, Mal.nem = *Malthonica nemorosa*, Mec.peu = *Mecophistes peusi*, Nom.exo = *Nomisia exornata*, Nom.rip = *Nomisia ripariensis*, Oed.api = *Oedothorax apicatus*, Ozy.san = *Ozyptila* cf. *sanctuaria*, Par.cri = *Pardosa cribrata*, Par.pal = *Pardosa paludicola*, Par.pra = *Pardosa prativaga*, Par.pro = *Pardosa proxima*, Par.vit = *Pardosa vittata*, Pll.dia = *Pellenes diagonalis*, Pll.nig = *Pellenes nigrociliatus*, Phl.fas = *Phlegra fasciata*, Pir.lat = *Pirata latitans*, Scy.tho = *Scytodes thoracica*, Tha.atr = *Thanatus atratus*, Tit.fla = *Titanoeca flavicoma*, Tit.tur = *Titanoeca turkmenia*, Tra.bar = *Trachyzelotes barbatus*, Tra.lyo = *Trachyzelotes lyonneti*, Tra.ped = *Trachyzelotes pedestris*, Tro.rur = *Trochosa ruricola*, Xys.cap = *Xysticus caperatus*, Xys.koc = *Xysticus kochi*, Zel.atr = *Zelotes atrocaernlens*, Zel.ilo = *Zelotes ilotarmn*, Zel.ten = *Zelotes tenuis*, Zod.fre = *Zodarion frenatum*, Zod.mor = *Zodarion morosum*.

Aulonia kratochvili, *Pardosa vittata*, *Pirata latitans* and *Trochosa ruricola* increased with increasing soil humidity, while those of xerophilic species (e.g., *Harpactea babori*, *Nomisia exornata*, *Xysticus caperatus*) decreased. Other environmental parameters were less influential, as only a few species were affected by either shading or vegetation cover. Of these, *Pellenes diagonalis* and *Xysticus kochi* responded negatively to increasing shading, while activity densities of *Brachythele denieri* increased.

DISCUSSION

Studies from Central Europe have demonstrated the importance of wetlands for the conservation of spider diversity (e.g., Weiss et al. 1998; Holec 2000), and Greenwood et al. (1995) showed that species diversity was higher in wetland habitats than in arable land. For the Mediterranean region analogous data are scarce, apart from very few studies that have assessed the conservation importance of reed beds (Schmidt et al. 2005) and freshwater habitats such as floodplains, river shores and humid grasslands (Buchholz 2009).

Spider assemblages of reed belts were less diverse than those of all other habitat types and showed lower evenness values, which indicate higher habitat dynamics and disturbance effects (Kratochwil & Schwabe 2001). This is most likely related to temporal flooding, and it appears that humid habitat types are inhabited by a few specialized species. These show high abundances (e.g., *Arctosa leopardus*: $n = 554$; *A. tbilisiensis*: $n = 245$) and are able to cope with disturbance due

Table 3.—Responses of spider species to selected environmental variables analyzed by GLM. Whether or not the variable had a positive or negative effect on species activity densities is indicated by "−" for decreasing (negative) and "+" for increasing (positive) effect. Significance levels are indicated as ***($P < 0.001$), **($P < 0.01$) or *($P < 0.05$). Abbreviated environmental predictor variables: soil.hum = soil humidity, cov.veg = vegetation cover. For a complete species list from Aladjagiola see Schröder et al. (2011). Only species with significant response are shown.

species	individuals	soil.hum	shading	cov.veg	R^2
Alopecosa albofasciata	79	− **	.	+ *	52.5
Arctosa leopardus	238	+ **	.	.	66.6
Arctosa tbilisiensis	110	+ *	.	.	76.8
Aulonia kratochvili	139	+ **	.	.	41.9
Brachythele denieri	11	.	+ *	.	44.2
Callilepis cretica	68	− *	.	.	32.6
Drassyllus praeficus	39	+ *	.	.	17.4
Haplodrassus signifer	32	+ *	.	.	41.8
Harpactea babori	16	− **	+ ***	.	76.6
Mecophistes peusi	10	.	.	− *	38.0
Nomisia exornata	21	− **	.	− *	70.8
Oedothorax apicatus	170	+ *	− *	.	66.5
Pardosa paludicola	52	+ *	.	.	83.2
Pardosa prativaga	182	+ *	.	.	45.1
Pardosa proxima	145	+ *	.	+ **	84.1
Pardosa vittata	61	+ ***	− ***	.	89.4
Pellenes diagonalis	18	.	− *	.	80.4
Pirata latitans	71	+ **	.	.	59.1
Scytodes thoracica	33	− *	.	.	75.4
Thanatus atratus	81	− **	.	+ *	45.0
Trachyzelotes pedestris	18	+ *	.	.	50.6
Trochosa ruricola	173	+ ***	.	.	78.9
Xysticus caperatus	51	− **	.	+ *	43.2
Xysticus kochi	42	.	− *	.	32.5
Zodarion frenatum	15	− *	.	.	37.0
Zodarion morosum	11	− *	− **	+ *	61.3

to flooding. Accordingly, functional evenness was lowest in reed belts as well as in humid grasslands. Although flooding was less common in humid grasslands than in reed belts, disturbance and habitat dynamics still affected species assemblages. With regard to functional evenness, lower values do not only indicate high habitat dynamics and disturbance effects, but also a less balanced niche occupancy (Schleuter et al. 2010) caused by the occurrence of rigorously hygrophilic species that occupy the same ecological niches. According to Villéger et al. (2008) both functional and species richness are closely related, and thus it is not surprising that humid sites had a lower functional diversity. In general, low functional diversity values can be explained by a lower number of available niches (Schirmel et al. 2012), which results from very homogeneous reed belts that provide only a minimally diverse habitat structure.

Conservation importance of wetland habitats.—Humid sites harbored numerous hyrophilic species (e.g., *Arctosa leopardus*, *A. tbilisiensis*, *Aulonia kratochvili*, *Oedothorax apicatus*, *Pardosa paludicola*, *P. prativaga*, *P. vittata*, *Pirata latitans* and *Trochosa ruricola*). Species assemblages could be clearly separated from those of dry habitats that included mostly xerophilic and photophilic species such as *Brachythele denieri*, *Harpactea babori*, *Nomisia exornata*, *Pellenes diagonalis*, *Scytodes thoracica*, *Xysticus caperatus* and *X. kochi*. A number of studies from Central Europe have shown that wetlands harbor unique spider assemblages that show a high sensitivity to altered soil humidity conditions (Bell et al. 1999; Bonn et al. 2002). However, due to lower precipitation and higher mean temperatures during the summer, effects on spider assemblages as well as activity levels might be much stronger in the Mediterranean region than in the temperate climate zone of Central and Northern Europe. Thus, the intensity of the anthropogenic impacts on the hydrological regime might be even more serious. In the case of the Aladjagiola wetland this would be crucial, since water withdrawal and consequent drying-out of freshwaters and adjacent wetland habitat types is highest by far during the summer (Taubert 1996).

Our study demonstrates that especially humid habitat types that suffer an ongoing habitat loss are worth protecting, as they harbor a unique spider assemblage. Analyses also showed that numerous species were constrained by soil humidity. These rigorously hygrophilic species depend strongly on the occurrence of wetland habitat types. Thus, it is likely that with proceeding habitat loss, the wetland assemblages will disappear. In addition, hygrophilic species may decline or, if it comes to the worst, they may even become extinct. Data for conservation issues—including ecological descriptions—are mostly rare in the eastern Mediterranean region. This is a drawback since updated datasets are urgently needed to, firstly, assess the conservation status of certain habitat types and, secondly, provide a basis for nature conservation strategies and habitat management objectives. Therefore, our results have particular importance for the northeastern Greek wetlands, which belong to a region that is of nationwide conservation importance due to its landscape diversity and biogeographical uniqueness (e.g., Jerrentrup et al. 1989;

Schröder et al. 2011). Considering the ongoing habitat loss and degradation, preservation and restoration of the remaining wetland habitats is urgently needed. We showed the importance of using spiders as a model group, knowing that spider species are an adequate surrogate for the conservation value of the total invertebrate fauna (Scott et al. 2006). On the other hand, data from Aladjagiola suggest that conservation importance does not only apply to invertebrates (e.g., Schumann 1996) but also to higher taxa (Donth 1996). Thus, there is an urgent need to drastically reduce the water withdrawal and to develop a more sustainable irrigation regime. Furthermore, land conversion planning must ensure the highest possible habitat diversity by conserving wetland habitats and thus preserving their unique spider assemblages.

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LITERATURE CITED

AG Boden. 1994. Bodenkundliche Kartieranleitung. Bundesanstalt für Geowissenschaften, Hannover.

Bell, D., G.E. Petts & J.P. Sadler. 1999. The distribution of spiders in the wooded riparian zone of three rivers in western Europe. Regulated Rivers-Research & Management 15:141–158.

Bell, J.R., D.A. Bohan, E.M. Shaw & G.S. Weyman. 2005. Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. Bulletin of Entomological Research 95:69–114.

Bonn, A., K. Hagen & D. Wohlgemuth-Von Reiche. 2002. The significance of flood regimes for carabid beetle and spider communities in riparian habitats—A comparison of three major rivers in Germany. River Research and Applications 18:43–64.

Britton, R.H. & A.J. Crivelli. 1993. Wetlands of southern Europe and North Africa: Mediterranean wetlands. Pp. 129–194. *In* Wetlands of the world: Inventory, ecology and management. Volume I. (D.F. Whigham, D. Dykyjová & S. Hejný, eds.). Kluwer Academic Publishers, Dordrecht.

Buchholz, S. 2009. Community structure of spiders in coastal habitats of a mediterranean Delta region (Nestos Delta, NE Greece). Animal Biodiversity and Conservation 32:101–115.

Buchholz, S. 2010. Ground spider assemblages as indicators for habitat structure in inland sand ecosystems. Biodiversity and Conservation 19:2565–2595.

Cardoso, P., S. Pekár, R. Jocqué & J.A. Coddington. 2011. Global patterns of guild composition and functional diversity of spiders. Plos One 6:e21710.

Cristofoli, S., G. Mahy, R. Kekenbosch & K. Lambeets. 2010. Spider communities as evaluation tools for wet heathland restoration. Ecological Indicators 10:773–780.

Donth, S. 1996. Die Herpetofauna des westlichen Nestos-Deltas und des angrenzenden Berglandes unter besonderer Berücksichtigung des Aladjagiola. Pp. 75–92. *In* Das Aladjagiola im Nestosdelta in Nordost-Griechenland. Beiträge zu Flora, Fauna, Landnutzung und Naturschutz. (H. Mattes & C. Lienau, eds.). Berichte aus dem Arbeitsgebiet Entwicklungsforschung 25, Münster.

Entling, W., M.H. Schmidt, S. Bacher, R. Brandl & W. Nentwig. 2007. Niche properties of Central European spiders: shading, moisture and the evolution of the habitat niche. Global Ecology and Biogeography 16:440–448.

Finch, O.-D. & R. Niedringhaus. 2010. Monitoring for the Habitats Directive and the importance of terrestrial invertebrates. Wadden Sea Ecosystem 26:53–56.

Greenwood, M.T., M.A. Bickerton & G.E. Petts. 1995. Spatial-distribution of spiders on the floodplain of the river Trent, UK—the role of hydrological setting. Regulated Rivers-Research & Management 10:303–313.

Hammer, Ö., D.A.T. Harper & P.D. Ryan. 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4:1–9.

Hecker, N., & R.T. Vives (eds.). 1995. The status of wetland inventories in the Mediterranean region. MedWet Publication/ IWRB Publication 38. Online at http://medwet.org/2010/02/the-status-of-wetland-inventories-in-the-mediterranean-region/

Holec, M. 2000. Spiders (Araneae) of the fishpond eulittoral zone. Ekológia 19:51–54.

Jerrentrup, H., J. Resch, E. Daroglou & E. Thielcke-Resch. 1989. Der Nestos—Leben zwischen Fluss und Meer. Naturerbe Verlag, Radolfzell.

Kratochwil, A. & A. Schwabe. 2001. Ökologie der Lebensgemeinschaften. Ulmer, Stuttgart.

Kremar, S. & E. Merdic. 2007. Comparison of the horse fly faunas of wetland areas in Croatia (Diptera: Tabanidae). Entomologia Generalis 30:235–244.

Laliberté, E. & P. Legendre. 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305.

Lienau, C. 1989. Griechenland—Geographie eines Staates der europäischen Südperipherie. Wissenschaftliche Buchgesellschaft, Darmstadt.

Mallinis, G., D. Emmanoloudis, V. Giannakopoulos, F. Maris & N. Koutsias. 2011. Mapping and interpreting historical land cover/land use changes in a Natura 2000 site using earth observational data. The case of Nestos delta, Greece. Applied Geography 31:312–320.

Mattes, H., & C. Lienau (eds.). 1996. Das Aladjagiola im Nestosdelta in Nordost-Griechenland. Beiträge zu Flora, Fauna, Landnutzung und Naturschutz. Berichte aus dem Arbeitsgebiet Entwicklungsforschung 25:1–138.

Nentwig, W., T. Blick, D. Gloor, A. Hänggi & C. Kropf. 2013. Spinnen Europas. Online at: www.araneae.unibe.ch

R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Online at http://www.r-project.org

Schirmel, J. & S. Buchholz. 2011. Response of carabid beetles (Coleoptera: Carabidae) and spiders (Araneae) to coastal heathland succession. Biodiversity and Conservation 20:1469–1482.

Schirmel, J., I. Blindow & S. Buchholz. 2012. Life-history trait and functional diversity patterns of ground beetles and spiders along a coastal heathland successional gradient. Basic and Applied Ecology 13:606–614.

Schleuter, D., M. Daufresne, F. Massol & C. Argillier. 2010. A user's guide to functional diversity indices. Ecological Monographs 80:469–484.

Schmidt, M.H., G. Lefebvre, B. Poulin & T. Tscharntke. 2005. Reed cutting affects arthropod communities, potentially reducing food for passerine birds. Biological Conservation 121:157–166.

Schröder, M., M. Chatzaki & S. Buchholz. 2011. The spider fauna of the Aladjagiola wetland complex (Nestos Delta, NE Greece)—a reflection of a unique zoogeographical transition zone in Europe. Biological Journal of the Linnean Society 102:217–233.

Schumann, B. 1996. Ökologische Untersuchungen zur Tagfalterfauna im Aladjagiola-Gebiet, Nordost-Griechenland. Pp. 104–113. *In* Das Aladjagiola im Nestosdelta in Nordost-Griechenland. Beiträge zu Flora, Fauna, Landnutzung und Naturschutz. (H. Mattes & C. Lienau, eds.). Berichte aus dem Arbeitsgebiet Entwicklungsforschung 25, Münster.

Scott, A.G., G.S. Oxford & P.A. Selden. 2006. Epigeic spiders as ecological indicators of conservation value for peat. Biological Conservation 127:420–428.

Taubert, M. 1996. Die Landwirtschaft im Aladjagiola. Pp. 26–41. *In* Das Aladjagiola im Nestosdelta in Nordost-Griechenland. Beiträge zu Flora, Fauna, Landnutzung und Naturschutz. (H. Mattes & C. Lienau, eds.). Berichte aus dem Arbeitsgebiet Entwicklungsforschung 25, Münster.

Vandewalle, M., F. de Bello, M.P. Berg, T. Bolger, S. Doledec, F. Dubs, C.K. Feld, R. Harrington, P.A. Harrison, S. Lavorel, P.M. da Silva, M. Moretti, J. Niemela, P. Santos, T. Sattler, J.P. Sousa, M.T. Sykes, A.J. Vanbergen & B.A. Woodcock. 2010. Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. Biodiversity and Conservation 19:2921–2947.

Villéger, S., N.W.H. Mason & D. Mouillot. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89:2290–2301.

Violle, C., M.L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel & E. Garnier. 2007. Let the concept of trait be functional! Oikos 116:882–892.

Weiss, I., E. Schneider & I. Andriescu. 1998. Die Spinnen des Biosphärenreservats Donau-Delta, Rumänien (Araehnida, Araneae). Linzer biologische Beiträge 30:263–275.

Zuur, A.F., E.N. Ieno, N.J. Walker, A.A. Saveliev & G.M. Smith. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, Berlin.

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Appendix I.—Individual number of spiders and life-history traits [according to Bell et al. 2005 (ballooning), Cardoso et al. 2011 (hunting), Nentwig et al. 2013 (female body size' mm)]. PM = pseudo-maquis, DGs = dry grassland – short growth, DGl = dry grassland – long growth, FR = fringes, RE = reed belts, HG = humid grassland, FL = fallow land.

Species	Life-history traits			Abundances							
	body size	hunting	ballooning	PM	DGs	DGl	FR	RE	HG	FL	sum.
Agelenidae											
Agelena orientalis C.L. Koch 1837	13.50	sheet web	less common	3	2	3	1	.	.	.	9
Malthonica nemorosa (Simon 1916)	10.75	sheet web	uncommon	8	.	1	9	.	2	.	20
Tegenaria angustipalpis Levy 1996	5.90	sheet web	uncommon	.	.	.	1	.	.	.	1
Amaurobidae											
Amaurobius erberi (Keyserling 1863)	9.50	sheet web	uncommon	1	.	.	1	.	.	.	2
Araneidae											
Agalenatea redii (Scopoli 1763)	7.50	orb web	uncommon	.	.	1	.	.	1	.	2
Araneus angulatus Clerck 1757	17.00	orb web	less common	.	1	.	.	.	.	.	1
Cercidia prominens (Westring 1851)	6.00	orb web	uncommon	.	.	.	.	.	1	.	1
Cyrtaraclne ixodoides (Simon 1870)	6.70	orb web	uncommon	.	.	.	.	1	.	.	1
Gibberanea bituberculata (Walckenaer 1802)	9.00	orb web	uncommon	.	.	1	5				6
G. gibbosa (Walckenaer 1802)	7.50	orb web	uncommon	1	.	.	.	.	.	.	1
Hypsosinga albovittata (Westring 1851)	4.00	orb web	eommon	.	1	2	.	.	.	1	4
Larinioides cornutus (Clerck 1757)	11.75	orb web	common	.	.	1	.	.	.	.	1
Mangora acalypha (Walckenaer 1802)	5.75	orb web	common	1	.	1	1	.	.	.	3
Neoscona adianta (Walckenaer 1802)	6.25	orb web	less common	.	.	1	5	.	1	1	8
Zilla diodia (Walckenaer 1802)	4.00	orb web	uncommon	1	.	.	.	.	.	.	1
Atypidae											
Atypus piceus (Sulzer 1776)	12.50	sensing web	uncommon	.	.	1	.	.	.	.	1
Clubionidae											
Clubiona lutescens Westring 1851	7.00	other hunters	less common	.	.	.	.	1	.	.	1
C. pluragmitis C.L. Koch 1843	9.50	other hunters	less common	.	.	.	1	.	.	.	1
Corinnidae											
Phrurolithus festivus (C.L. Koch 1835)	3.00	ground hunters	uncommon	3	2	2	10	2	3	.	22
P. szilyi Herman 1879	2.50	ground hunters	uncommon	3	1	1	1	.	.	.	6
Dictynidae											
Archaeodictyna consecuta (O.P.-Cambridge 1872)	2.00	space web	uncommon	1	.	.	.	1	.	.	2
Dictyna arundinacea (Linnaeus 1758)	3.25	space web	common	.	.	.	.	.	9	.	9
Dysderidae											
Dysdera longirostris Doblika 1853	7.00	specialists	uncommon	1	.	.	5	.	4	.	10
Harpactea babori (Nosek 1905)	7.60	specialists	uncommon	27	1	1	14	.	.	.	43
Stalagtia thaleriana Chatzaki & Arnedo 2006	5.50	specialists	uncommon	.	1	.	.	.	.	.	1
Eresidae											
Eresus kollari Rossi 1846	12.50	sheet web	uncommon	2	2	5	.	2	.	.	11
Filistatidae											
Pritha nana (Simon 1868)	3.45	sensing web	uncommon	5	1	.	.	.	.	.	6
Gnaphosidae											
Aphantaulax cincta (L. Koch 1866)	6.00	ground hunters	uncommon	.	1	.	.	.	.	.	1
A. trifasciata (O.P.-Cambridge 1872)	5.50	ground hunters	uncommon	.	.	.	1	.	.	.	1

Appendix—Continued.

Species	Life-history traits			Abundances							
	body size	hunting	ballooning	PM	DGs	DGl	FR	RE	HG	FL	sum.
Callilepis cretica (Roewer 1928)	5.50	ground hunters	uncommon	36	32	54	66	.	1	.	189
Camillina metellus (Roewer 1928)	4.00	ground hunters	uncommon	.	.	.	.	.	.	2	2
Drassodes lapidosus (Walckenaer 1802)	12.00	ground hunters	uncommon	.	1	5	1	1	1	3	12
D. pubescens (Thorell 1856)	7.50	ground hunters	uncommon	.	1	.	1	3	2	.	7
Drassyllus lutetianus (L. Koch 1866)	5.00	ground hunters	common	.	.	.	.	2	1	1	4
D. praeficus (L. Koch 1866)	6.00	ground hunters	common	2	13	6	24	15	36	6	102
Gnaphosa lucifuga (Walckenaer 1802)	15.50	ground hunters	less common	.	.	.	6	1	1	32	40
Haplodrassus dalmatensis (L. Koch 1866)	6.00	ground hunters	uncommon	.	2	5	2	.	.	5	14
H. invalidus (O.P.-Cambridge 1872)	7.50	ground hunters	uncommon	.	1	.	.	.	.	.	1
H. minor (O.P.-Cambridge 1879)	3.50	ground hunters	uncommon	.	.	.	1	.	14	.	15
H. signifer (C.L. Koch 1839)	8.50	ground hunters	uncommon	.	11	6	14	6	37	4	78
Micaria albovittata (Lucas 1846)	6.25	ground hunters	common	.	.	.	.	2	14	1	17
M. coarctata (Lucas 1846)	5.40	ground hunters	common	.	.	.	1	.	.	.	1
M. guttulata (C.L. Koch 1839)	2.95	ground hunters	common	1	3	5	1	.	.	.	10
M. pulicaria (Sundevall 1831)	3.50	ground hunters	common	.	.	.	2	7	5	.	14
Nomisia exornata (C.L. Koch 1839)	6.00	ground hunters	uncommon	4	37	11	7	.	.	.	59
N. ripariensis (O.P.-Cambridge 1872)	7.30	ground hunters	uncommon	.	19	5	5	.	4	8	41
Trachyzelotes barbatus (L. Koch 1866)	8.30	ground hunters	common	.	7	7	4	.	4	.	22
T. lyonneti (Audouin 1826)	7.10	ground hunters	common	.	1	.	7	.	7	2	17
T. malkini Platnick & Murphy 1984	6.95	ground hunters	common	.	.	1	1	.	2	2	6
T. pedestris (C.L. Koch 1837)	7.50	ground hunters	common	.	.	3	4	2	32	.	41
Zelotes argoliensis (C.L. Koch 1839)	6.35	ground hunters	common	.	1	.	4	.	.	.	5
Z. atrocaeruleus (Simon 1878)	7.00	ground hunters	common	.	2	1	16	10	33	.	62
Z. caucasius (L. Koch 1866)	5.50	ground hunters	common	.	1	1	.	.	.	1	3
Z. gracilis (Canestrini 1868)	2.00	ground hunters	common	.	.	.	1	.	.	.	1
Z. ilotarum (Simon 1884)	7.45	ground hunters	common	3	11	2	.	.	.	1	17
Z. longipes (L. Koch 1866)	6.00	ground hunters	common	.	.	1	1	.	2	1	5
Z. segrex (Simon 1878)	5.10	ground hunters	common	.	12	6	1	.	.	.	19
Z. tenuis L. Koch 1866	6.55	ground hunters	common	3	6	6	3	.	3	.	21
Hahniidae											
Antistea elegans (Blackwall 1841)	3.00	sheet web	uncommon	.	.	.	.	1	5	.	6
Linyphiidae											
Acartauchenius scurrilis (O.P.-Cambridge 1872)	1.85	other hunters	uncommon	.	.	1	.	.	.	3	4
Ceratinella brevipes (Westring 1851)	1.70	other hunters	less common	1	.	.	.	2	.	.	3
C. brevis (Wider 1834)	2.00	other hunters	less common	1	.	.	.	1	2	.	4
Diplostyla concolor (Wider 1834)	2.75	sheet web	common	.	.	.	.	.	15	.	15
Enteclara acuminata (Wider 1834)	2.20	other hunters	less common	1	.	.	.	.	.	.	1
Erigone dentipalpis (Wider 1834)	2.30	other hunters	common	1	2	.	.	2	1	1	7
Frontinellina frutetorum (C.L. Koch 1834)	5.50	sheet web	less common	.	.	1	.	.	.	.	1
Gnathonarium dentatum (Wider 1834)	2.40	other hunters	common	.	2	.	.	16	.	.	18
Gongylidiellum murcidum Simon 1884	1.60	other hunters	common	1	.	.	.	.	.	.	1
Gongylidium rufipes (Linnaeus 1758)	3.40	other hunters	uncommon	.	.	.	2	.	.	.	2
Mecophistes peusi Wunderlich 1972	1.60	other hunters	uncommon	11	15	3	1	.	.	.	30
Meioneta fuscipalpa (C.L. Koch 1836)	1.90	sheet web	less common	.	.	.	.	.	.	1	1
M. pseudorurestris (Wunderlich 1980)	1.80	sheet web	less common	.	.	1	.	2	2	2	7
Neriene clathrata (Sundevall 1830)	4.35	sheet web	common	1	.	.	1	.	.	.	2
Oedothorax apicatus (Blackwall 1850)	2.75	other hunters	common	.	8	.	2	389	5	.	404
Pelecopsis elongata (Wider 1834)	2.05	other hunters	common	.	.	.	.	1	.	.	1
P. parallela (Wider 1834)	1.65	other hunters	common	1	1	.	.	.	.	6	8
Pocadicnemis juncea Locket & Millidge 1953	1.90	other hunters	uncommon	.	.	.	.	2	2	.	4
Prinerigone vagans (Audouin 1826)	2.10	other hunters	common	.	1	.	.	17	2	.	20
Scutpelecopsis kransi (Wunderlich 1980)	1.40	other hunters	common	.	1	.	.	.	.	.	1
Syaedra gracilis (Menge 1869)	2.45	other hunters	uncommon	3	.	.	.	.	.	.	3
Trichoncus hackmani Millidge 1955	2.10	other hunters	uncommon	.	1	5	.	3	1	.	10
Walckenaeria alticeps (Denis 1952)	2.35	other hunters	common	2	.	.	3	.	.	.	5
W. vigilax (Blackwall 1853)	2.55	other hunters	common	.	.	.	.	3	.	.	3
Liocranidae											
Agraecina lineata (Simon 1878)	8.00	ground hunters	uncommon	.	.	1	.	.	1	.	2

Appendix—Continued.

Species	Life-history traits			Abundances							
	body size	hunting	ballooning	PM	DGs	DGl	FR	RE	HG	FL	sum.
Agroeca cuprea Menge 1873	4.00	ground hunters	uncommon	.	.	.	4	.	1	.	5
A. lusatica (L. Koch 1875)	6.00	ground hunters	uncommon	.	.	.	.	.	9	.	9
Liocranoeca striata (Kulczyn'ski 1882)	5.00	ground hunters	uncommon	.	.	.	.	.	38	.	38
Lycosidae											
Alopecosa albofasciata (Brullé 1832)	11.00	ground hunters	less common	58	16	14	51	5	2	31	177
A. pentheri (Nosek 1905)	9.00	ground hunters	less common	.	2	.	.	.	.	1	3
Arctosa leopardus (Sundevall 1833)	9.00	ground hunters	less common	.	.	.	3	411	143	.	557
A. perita (Latreille 1799)	7.75	ground hunters	common	.	.	.	1	8	1	4	14
A. tbilisiensis Mcheidze 1946	6.50	ground hunters	less common	.	.	.	3	28	217	2	250
Aulonia kratochvili Dunin, Buchar & Absolon 1986	5.00	ground hunters	less common	.	.	36	93	62	149	.	340
Geolycosa vultuosa (C.L. Koch 1838)	18.50	ground hunters	less common	.	2	1	.	.	.	.	3
Hogna radiata (Latreille 1817)	18.50	ground hunters	less common	11	4	12	4	1	.	1	33
Pardosa agrestis (Westring 1861)	7.50	ground hunters	common	.	.	.	.	3	.	.	3
P. agricola (Thorell 1856)	6.75	ground hunters	common	.	.	.	.	2	.	1	3
P. cribrata Simon 1876	6.25	ground hunters	common	.	.	.	4	82	61	36	183
P. hortensis (Thorell 1872)	5.25	ground hunters	common	.	.	2	3	13	4	.	22
P. monticola (Clerck 1757)	5.00	ground hunters	common	.	.	.	.	4	.	.	4
P. paludicola (Clerck 1757)	8.50	ground hunters	common	.	.	.	.	4	112	.	116
Pardosa prativaga (L. Koch 1870)	5.00	ground hunters	common	.	.	.	95	303	45	.	443
P. proxima (C.L. Koch 1847)	6.00	ground hunters	common	.	.	.	2	161	164	19	346
P. vittata (Keyserling 1863)	6.30	ground hunters	common	.	.	.	.	48	91	.	139
Pirata latitans (Blackwall1841)	4.50	ground hunters	common	.	.	.	35	63	70	.	168
P. piraticus (Clerck 1757)	6.80	ground hunters	common	.	.	.	.	1	.	.	1
Trebacosa europaea Szinétar & Kancsal 2007	6.25	ground hunters	uncommon	.	.	.	.	7	.	.	7
Trochosa ruricola (De Geer 1778)	11.50	ground hunters	less common	1	.	.	28	94	276	3	402
T. terricola Thorell 1856	11.50	ground hunters	common	.	.	.	.	.	4	.	4
Xerolycosa miniata C.L. Koch 1834	7.00	ground hunters	uncommon	.	.	.	.	1	10	1	12
Mimetidae											
Ero furcata (Villers 1789)	4.00	specialists	common	.	.	.	1	.	.	.	1
Nemesidae											
Brachythele denieri (Simon 1916)	12.50	sensing web	uncommon	17	2	11	4	.	.	.	34
Oonopidae											
Silhouettella loricatula (Roewer 1942)	2.00	ground hunters	uncommon	2	.	.	.	.	.	.	2
Oxyopidae											
Oxyopes heterophthalmus (Latreille 1804)	6.00	other hunters	common	.	.	.	.	.	.	1	1
O. mediterraneus Levy 1999	6.75	other hunters	common	.	2	.	.	.	.	1	3
Philodromidae											
Philodromus pulchellus Lucas 1846	3.85	other hunters	common	.	1	.	.	.	.	.	1
Thanatus atratus Simon 1875	5.30	other hunters	uncommon	38	25	59	33	12	3	36	206
T. striatus C.L. Koch 1845	5.10	other hunters	uncommon	.	.	.	.	.	7	.	7
Tibellus oblongus (Walckenaer 1802)	9.00	other hunters	common	.	.	1	2	.	.	.	3
Pisauridae											
Pisaura mirabilis (Clerck 1757)	13.50	sheet web	common	6	4	3	11	1	3	4	32
Salticidae											
Aelurillus v-insignitus (Clerck 1757)	5.95	other hunters	uncommon	1	5	1	1	.	.	1	9
Ballus chalybeius (Walckenaer 1802)	3.80	other hunters	uncommon	.	1	.	.	.	.	.	1
Chalcoscirtus infimus (Simon 1868)	2.50	other hunters	uncommon	2	5	5	3	.	.	1	16
Euophrys frontalis (Walckenaer 1802)	3.50	other hunters	uncommon	1	.	.	.	.	.	.	1
E. rufibarbis (Simon 1868)	4.25	other hunters	uncommon	1	.	.	.	.	.	.	1
Evarcha arcuata (Clerck 1757)	7.00	other hunters	uncommon	.	.	.	.	.	1	.	1
E. jucunda (Lucas 1846)	6.10	other hunters	uncommon	2	.	.	.	.	.	.	2
Heliophanus auratus C.L. Koch 1835	4.85	other hunters	uncommon	.	.	.	.	1	.	.	1
H. lineiventris Simon 1868	4.95	other hunters	uncommon	.	.	.	.	.	.	1	1
Icius hamatus (C.L. Koch 1846)	5.40	other hunters	common	.	.	1	.	.	.	.	1
Leptorchestes nuntilloides (Lucas 1846)	3.70	other hunters	uncommon	1	.	.	.	.	.	.	1
Macaroeris nidicolens (Walckenaer 1802)	5.00	other hunters	common	1	.	.	.	.	.	.	1
Neaetha membrosa (Simon 1868)	4.50	other hunters	uncommon	.	2	.	1	.	.	.	3
Neon rayi (Simon 1875)	2.50	other hunters	uncommon	1	.	.	.	.	.	.	1

Appendix—Continued.

Species	Life-history traits			Abundances							
	body size	hunting	ballooning	PM	DGs	DGl	FR	RE	HG	FL	sum.
Pellenes diagonalis (Simon 1868)	6.50	other hunters	uncommon	.	36	10	.	.	.	.	46
P. nigrociliatus (Simon 1875)	5.30	other hunters	uncommon	.	7	11	.	.	2	3	23
P. seriatus (Thorell 1875)	7.75	other hunters	uncommon	.	.	.	1	.	.	.	1
Philaeus chrysops (Poda 1761)	7.50	other hunters	uncommon	.	1	.	.	.	.	.	1
Phlegra fasciata (Hahn 1826)	6.40	other hunters	common	.	11	6	11	2	3	6	39
P. lineata (C.L. Koch 1846)	3.85	other hunters	less common	.	.	1	.	.	1	.	2
Pseudeuophrys obsoleta (Simon 1868)	4.00	other hunters	less common	6	.	1	.	.	.	.	7
Sitticus penicillatus (Simon 1875)	3.75	other hunters	uncommon	.	.	.	.	.	.	2	2
Synageles dalmaticus (Keyserling 1863)	3.00	other hunters	common	1	.	.	.	.	.	.	1
Talavera aequipes (O.P.-Cambridge 1871)	2.50	other hunters	uncommon	.	.	.	.	.	2	1	3
Scytodidae											
Scytodes thoracica (Latreille 1802)	5.00	other hunters	uncommon	35	4	7	42	1	.	.	89
Sparassidae											
Micrommata virescens (Clerck 1757)	13.50	other hunters	uncommon	.	1	.	.	.	.	.	1
Tetragnathidae											
Pachygnatha clercki Sundevall 1823	5.75	orb web	common	.	.	.	.	1	.	.	1
P. degeeri Sundevall 1830	3.85	orb web	common	.	.	.	2	8	1	.	11
Tetragnatha montana Simon 1874	8.50	orb web	common	.	.	.	1	.	.	.	1
Theridiidae											
Asagena phalerata (Panzer 1801)	4.75	space web	less common	.	2	4	6	1	2	3	18
Crustulina sticta (O.P.-Cambridge 1861)	2.50	space web	less common	.	.	.	.	1	1	.	2
Dipoena coracina (C.L. Koch 1837)	2.00	space web	common	.	.	2	.	1	5	.	8
Enoplognatha thoracica (Hahn 1833)	3.75	space web	common	1	.	.	1	1	.	1	4
Episinus truncatus Latreille 1809	5.00	space web	uncommon	1	.	.	.	.	.	.	1
Euryopis episinoides (Walckenaer 1847)	3.00	space web	common	.	.	1	.	.	.	.	1
E. quinqueguttata Thorell 1875	2.50	space web	common	2	.	1	1	.	.	1	5
Latrodectus tredecimguttatus (Rossi 1790)	13.00	space web	less common	.	.	.	.	.	.	1	1
Pholcomma gibbum (Westring 1851)	1.70	space web	uncommon	2	.	.	.	.	.	.	2
Robertus mediterraneus Eskov 1987	3.50	space web	less common	.	.	.	.	.	1	.	1
Steatoda albomaculata (De Geer 1778)	6.00	space web	less common	.	4	.	.	.	.	.	4
Theridion cinereum Thorell 1875	3.20	space web	common	.	.	.	1	.	.	1	2
Thomisidae											
Monaeses israeliensis Levy 1973	8.50	ambush hunters	uncommon	.	.	.	1	.	.	.	1
Ozyptila cf. *sanctuaria*	3.50	ambush hunters	common	.	9	12	4	.	.	6	31
O. praticola (C.L. Koch 1837)	3.50	ambush hunters	common	.	.	.	3	.	.	.	3
O. simplex (O.P.-Cambridge 1862)	4.50	ambush hunters	common	.	.	.	.	1	.	.	1
Runcinia grammica (C.L. Koch 1837)	6.35	ambush hunters	uncommon	.	.	.	.	.	.	2	2
Synema plorator (O.P.-Cambridge 1872)	5.90	ambush hunters	less common	.	2	7	.	.	.	.	9
Xysticus caperatus Simon 1875	7.30	ambush hunters	common	9	4	37	34	1	1	24	110
X. cristatus (Clerck 1757)	6.35	ambush hunters	common	.	1	1	1	.	1	.	4
X. gallicus Simon 1875	9.00	ambush hunters	common	.	2	2	.	.	1	1	6
X. graecus C.L. Koch 1837	8.45	ambush hunters	common	.	.	1	.	.	.	.	1
X. kempelini Thorell 1872	6.55	ambush hunters	common	2	2	.	10	.	1	.	15
X. kochi Thorell 1872	8.45	ambush hunters	common	2	40	32	7	4	14	10	109
X. luctator L. Koch 1870	8.50	ambush hunters	common	.	.	.	1	.	.	.	1
X. robustus (Hahn 1832)	9.50	ambush hunters	common	.	4	3	.	.	.	1	8
X. xerodermus Strand 1913	7.75	ambush hunters	common	.	2	.	.	.	2	.	4
Titanoecidae											
Nurscia albomaculata (Lucas 1846)	10.50	space web	uncommon	.	2	2	5	8	8	2	27
Titanoeca flavicoma L. Koch 1872	6.10	space web	uncommon	.	48	84	5	11	4	26	178
T. turkmenia Wunderlich 1995	4.80	space web	uncommon	.	.	.	.	.	.	7	7
Zodariidae											
Zodarion epirense Brignoli 1984	4.25	specialists	uncommon	.	.	1	2	.	.	2	5
Z. frenatum Simon 1884	4.00	specialists	uncommon	2	11	12	9	.	2	10	46
Z. granulatum Kulczyn'ski 1908	2.30	specialists	uncommon	.	.	.	1	.	.	.	1
Z. morosum Denis 1935	5.55	specialists	uncommon	.	9	9	3	.	1	4	26
Z. thoni Nosek 1905	4.10	specialists	uncommon	.	2	.	.	.	.	.	2
Zoridae											
Zora armillata Simon 1878	5.25	ground hunters	common	.	.	.	1	1	.	.	2
Z. parallela Simon 1878	4.95	ground hunters	common	.	.	1	.	.	.	.	1
Z. silvestris Kulczyn'ski 1897	3.75	ground hunters	common	.	.	.	.	1	.	.	1

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Love is in the air and on the ground: olfactory and tactile cues elicit visual courtship behavior by *Cyrba* males (Araneae: Salticidae)

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Abstract. Jumping spiders (Salticidae) are known for their complex eyes and exceptional spatial vision, but less is known about the role of chemoreception in salticid behavior. Here we investigate whether olfactory pheromones (i.e., airborne chemical signals) from conspecific spiders and their draglines elicit the display behavior typically performed during vision-based courtship from the males of *Cyrba algerina* (Lucas 1846) and *C. ocellata* (Kroneberg 1875). We used conspecific and heterospecific spiders and their draglines as potential sources of chemical cues. We show that olfactory cues from conspecific females, but not conspecific males or heterospecific females, effectively elicit vision-based courtship from the males of both *Cyrba* species. These results demonstrate that *C. algerina* and *C. ocellata* males make display decisions on the basis of species- and sex-specific olfactory information. Moreover, even in the absence of a conspecific female spider, female draglines suffice as a source of olfactory pheromones, illustrating the difficulty of ruling out olfaction when testing for chemotactile pheromones.

Keywords: Jumping spiders, mate-identification, olfaction, pheromones

It is common for animals to use pheromones in species and sex identification (Bradbury & Vehrenchamp 2011; Steiger et al. 2011). However, the literature on pheromones is dominated by research on insects (Shorey 1976; Cardé & Millar 2004; Symonds & Elgar 2008), (ref), with considerably less being known about the role of sex pheromones in the biology of spiders (Gaskett 2007; Schulz 2013).

Arachnologists often make a distinction between chemotactile and olfactory pheromones in the spider literature (Barth 2001; Foelix 2011), the former depending on contact chemoreception, and the latter on the detection of airborne volatile compounds. Although experiments that allow for contact chemoreception in the presence of web, nest or dragline silk are common, only a few spider species have been shown experimentally to rely on olfactory communication (Gaskett 2007; Uhl 2013).

Jumping spiders (Salticidae) are better known for their exceptional capacity for spatial vision (Land & Nilsson 2002; Harland et al. 2012), and for their intricate and elaborate vision-based behavior (Foelix 2011), including vision-based courtship displays (Jackson & Pollard 1997). However, numerous examples are also known of salticids expressing refined abilities for using chemical, acoustic, tactile, and percussion signals during intraspecific interactions (Jackson & Pollard 1997; Elias et al. 2010). Although experiments allowing for response to chemotaetile pheromones are more common in the salticid literature (Uhl 2013), 30 species from 17 salticid genera are currently known to use specifically olfactory sex pheromones (Willey & Jackson 1993; Jackson & Cross 2011; Nelson et al. 2012; Cerveira & Jackson 2013).

Our interest here is in a particular cross-modality effect that until now has only been described in one salticid species, *Evarcha culicivora* Wesolowska & Jackson 2003 (Cross & Jackson 2013). In *E. culicivora,* chemoreception elicits vision-based courtship. This cross-modality effect is of particular interest because it appears to be contrary to Foelix's (2011) hypothesis that chemotactile pheromones function primarily by eliciting the spider's courtship displays and olfactory pheromones function primarily by attracting the spider to a potential mate's location.

As a step toward determining how common it is within the Salticidae for pheromones to elicit vision-based display, we carried out experiments using *Cyrba algerina* (Lucas 1846) and *C. ocellata* (Kroneberg 1875). The rationale for using these two species comes from previous research showing that the males of these species are attracted to the odor of conspecific females (Cerveira & Jackson 2013). However, whether chemical stimuli might elicit vision-based displays in these species has not been investigated before.

We have also been interested in the distinction between olfactory and chemotactile pheromones. Two classes of sensory organs mediate chemoreception in spiders. Tip-pore sensilla are specialized hairs on the spider's palps and forelegs that function primarily as contact chemoreceptors (Foelix 1970; Harris and Mill 1973; Tichy et al. 2001; Jiao et al. 2011), whereas tarsal organs are small pits, or sometimes rods, on the dorsal side of each leg tarsus that function primarily as olfactory receptors (Foelix & Chu-Wang 1973; Dumpert 1978; but see Ehn & Tichy 1996). However, when only the spider's behavior is recorded during spider-pheromone experiments, we need to acknowledge the difficulties that can arise when trying to determine whether the behavior observed is mediated by olfaction or by contact chemoreception. Although we can easily rule out contact chemoreception by ensuring that the test spider does not touch the putative source of the chemical stimuli, finding methods that test for chemotactile pheromones while preventing olfaction is a formidable problem. Solving this problem is not our goal, but we illustrate its relevance by showing that dragline odor can elicit vision-based courtship display.

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METHODS

All test spiders were taken from laboratory cultures (second and third generation; origin for *C. algerina*, Sintra, Portugal; for *C. ocellata*, Mbita Point, Kenya). Voucher specimens of *C. algerina* and *C. ocellata* have been deposited at the National Museum of Kenya (Nairobi), the Museum of Natural History (Wroelaw University, Poland) and the Florida State Collection of Arthropods (Gainesville, Florida). We adopted standard spider-laboratory rearing and testing procedures and provide only critical details here. Further details can be found elsewhere (see: Jackson & Hallas 1986; Cerveira & Jackson 2011, 2013).

Spiders were kept individually in clear plastic cages (diameter 55 mm, height 100 mm). A hole in the top was used for introducing prey and another hole covered with a metal screen allowed air to enter the cage. The screen was heat-sealed to the plastic beside the hole. To ensure that the spider always had access to water, we made a hole centered in the bottom of the cage and placed the cage on a plastic pot filled with water. A cotton roll ("dental wick") was positioned in this hole with one end protruding a few millimeters into the cage and the other extending outside the cage into the pot of water. We replaced the cotton rolls whenever mold appeared on them. We also removed prey remains and cleaned the cages frequently. Spiders were maintained on a mixed diet of spiders (*Argyrodes* spp. and *Pardosa* spp.) and non-biting midges (Chaoboridae and Chironomidae) collected from the field as needed.

For environmental enrichment, which is known to be important when rearing salticids for behavioral experiments in the laboratory (Carducci & Jakob 2000), each cage contained a piece of dark cardboard folded in a bellows shape and kept in place inside the cage by a thin bamboo stick that pierced the folds in the cardboard like a skewer (Fig. 1). Resident spiders frequently walked on, and captured prey on, the cardboard. Resident spiders also used the darker recesses in the folded eardboard as nest-building and resting sites. Only adult males were used as test spiders because, consistent with a trend among animals as a whole (Trivers 1972; Andersson 1994), *Cyrba* males are more active than females at displaying during courtship (Jackson 1990).

Our test apparatus was a plastic Petri dish (diameter 60 mm) sitting in the center of a glass-top table (300 mm × 300 mm, glass 5 mm thick). Wooden legs held the table top 270 mm above the laboratory bench (Fig. 2). The Petri dish had two holes (diameter 16 mm), one in its base (stimulus opening) and the other in the lid (entrance opening). The holes were plugged with perforated rubber stoppers. The narrower end of the stopper was the same diameter (16 mm) as the hole and therefore fit evenly with the inner surfaee of the dish. The hole in each stopper held a glass tube (diameter 8 mm; length 45 mm). The tube in the entrance-opening stopper was called the "entrance tube" and the hole in the stimulus-opening stopper was called the "stimulus tube." A matching hole of similar diameter (18 mm) in the tabletop allowed the stimulus tube to fit through the table top and connect via silicone tubing to a glass tube (diameter 15 mm; length 90 mm) called the "odor chamber." The odor chamber was in turn connected via silicone tubing to an air pump. A Matheson FM-1000 flow meter between the pump and the odor chamber maintained

Figure 1.—Salticid maintenance cage. Each cage (diameter 55 mm, height100 mm) contained a piece of dark cardboard folded in a bellows shape kept in place by a thin bamboo stick pierced through the cardboard folds. A hole in the top was used for introducing prey. Water provided via cotton wick partially immersed in water and extending through base of cage.

constant airflow set at 1500 ml/min. There was no evidence to suggest that this airflow setting had any adverse effects on the test spider's behavior. We used nylon netting to cover the openings of the glass tubes and to ensure the spiders could not leave the Petri dish.

Three testing methods were used with both *Cyrba* species: olfactory, tactile and olfactory-tactile tests. In olfactory tests, there was either a source spider or its draglines in the odor chamber, but no draglines were present in the Petri dish. The odor chamber was empty during tactile tests, but the Petri dish contained draglines from the source spider. In olfactory-tactile tests, the odor chamber contained a conspecific female and the Petri dish contained draglines from a heterospecific female. In olfactory tests and in tactile tests, we used males and females of both species as odor sources. However, in olfactory-tactile tests, only female spiders and their draglines provided odor cues.

We collected draglines with a glass Petri dish (diameter 60 mm) lined with two circular sheets of blotting paper (diameter 60 mm), one for the inside base and one for the inside lid. The blotting paper was held in place by four squares (each side 10 mm) of double-sided sticky tape spaced evenly

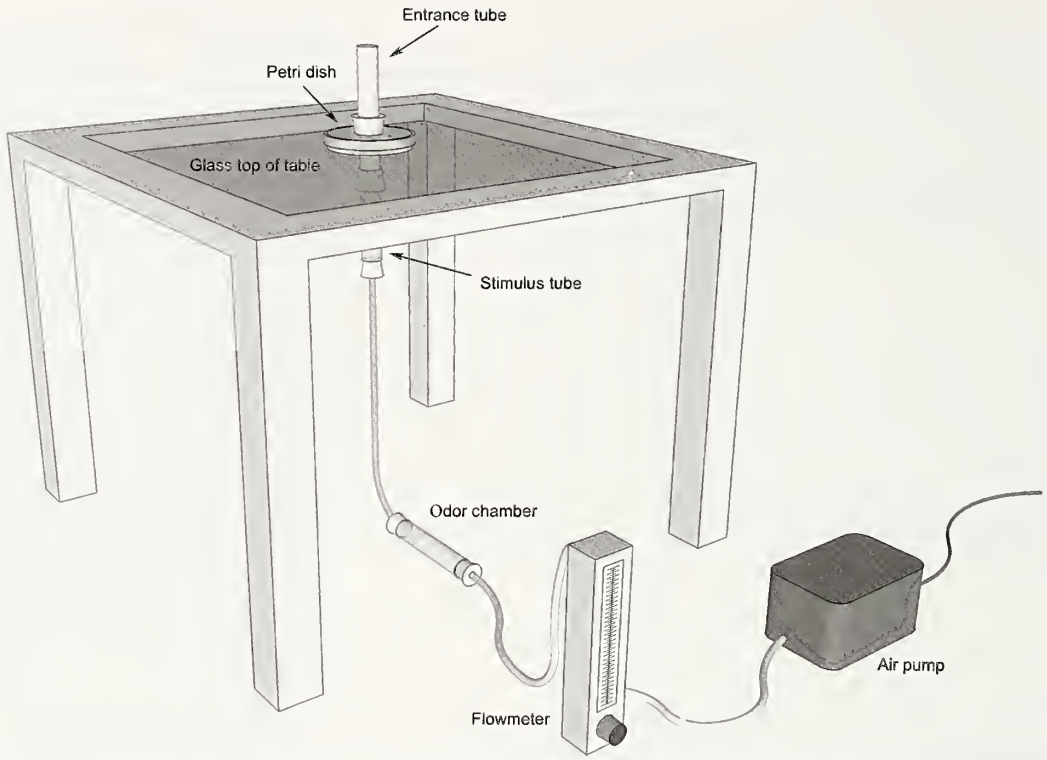

Figure 2.—Apparatus for display-elicitation testing. Three test types were performed: olfactory, tactile and olfactory-tactile. Depending on test type, odor chamber and Petri dish may contain source spider or the source-spider's draglines. See text for details.

around the inside perimeter of the dish. At 0800 h the source spider was put in the dish, and the dish was then oriented upright using a clamp so that neither of the two circles of blotting paper was above the other. Before testing began on the following day, we opened the Petri dish, removed the source spider and the sticky tape, chose one of the two pieces of blotting-paper circles at random and placed this circle silk-side-up on the base of the Petri dish or rolled it up loosely and inserted it into the odor chamber. The odor souree, either a source spider or its draglines, was put in the odor chamber 15 min before testing began.

Test spiders were introduced into the apparatus using a glass tube (length 50 mm, diameter 16 mm) with each end plugged by a rubber stopper. After a 5-min acclimation period, we removed one of the stoppers and inserted the tube into the entrance opening of the Petri dish. If the spider was still in the tube after 2 min, we gently nudged the spider using a soft brush so that it entered the Petri dish.

Data collection began when the spider entered the dish and continued for 10 min. During the test, we recorded all instances of test spiders displaying. We defined 'display' as behavior typically seen in vision-based intraspecific interactions, but only rarely seen in any other context. Here we briefly describe four specific displays (quiver-swim-wave, twitch-abdomen, posture, and dance) that were observed during our experiments, but additional details concerning these displays can be found elsewhere (Jackson 1990). We never saw any of these displays during preliminary testing of *Cyrba* individuals in the apparatus with clean blotting paper in the Petri dish and the odor ehamber empty.

Quiver-swim-wave is a modified form of swim-wave, and swim-wave is characteristic of both sexes of *Cyrba* during normal locomotion. When swim-waving, both sexes of *Cyrba* move their forelegs up and to the side and then, without pausing, move them more slowly down and inward. While moving down and inward, the forelegs move across the substratum. At the end of the cycle, the tarsi of the left and right legs are either pointing forward about parallel to each other or converging toward each other. Quiver-swim-waving is similar to swim-waving except for the distinctive quivering motion of the legs during the down-inward phase. Every test spider that engaged in display performed quiver-swim-waving regardless of whether it also performed any of the other three displays.

A spider twitches its abdomen in bouts lasting 1–10 s. During a bout, the spider repeatedly and rapidly flexes its abdomen up from parallel to the substratum and then, after a momentary pause, forcefully moves it back down to parallel to the substratum.

While walking or standing, the spider postures by holding its forelegs elevated and stationary. The two legs are about parallel to the substratum and to each other, and they point straight ahead or converge somewhat in front of the spider.

Dancing is any of three distinctive styles of stepping. Sometimes the dancing spider traces a zigzagging path forward. At other times, it repeatedly makes a semicircle in one direction and then in the other direction. Another style of dancing consists of repeatedly stepping forward and then backwards. Spiders always posture while dancing.

Experiments were carried out under dim light, since it is known from other studies that *Cyrba* may become non-responsive in olfactometer experiments carried out under high levels of ambient light (Cerveira & Jackson 2011). We placed the apparatus inside a brown wooden box (length 500 mm,

Table 1.—Response by adult males of *Cyrba algerina* and *C. ocellata* in three display-elicitation experiments using conspecific and heterospecific males and females as potential pheromone sources (tactile: draglines present, no additional odor cue present in odor chamber; olfactory: draglines absent, odor cue present in odor chamber; olfactory-tactile: draglines and additional odor cue present in odor chamber). See text and Fig. 2 for details on testing methods. $n = 25$ for each row.

Test	Test spider	Cue in stimulus chamber	Cue in petri dish	No that displayed
Olfactory	*C. algerina* male	*C. algerina* female	None	6
		C. ocellata female	None	0
		C. algerina male	None	0
		C. algerina female draglines	None	3
		C. ocellata female draglines	None	0
		C. ocellata male draglines	None	0
	C. ocellata male	*C. ocellata* female	None	8
		C. algerina female	None	0
		C. ocellata male	None	0
		C. ocellata female draglines	None	3
		C. algerina female draglines	None	0
		C. ocellata male draglines	None	0
Tactile	*C. algerina* male	None	*C algerina* female draglines	18
		None	*C. ocellata* female draglines	0
		None	*C. algerina* male draglines	0
	C. ocellata male	None	*C. ocellata* female draglines	22
		None	*C. algerina* female draglines	0
		None	*C. ocellata* male draglines	0
Olfactory-tactile	*C. algerina* male	*C. algerina* female	*C. ocellata* female draglines	16
	C. ocellata male	*C. ocellata* female	*C. algerina* female draglines	19

width 500 mm, height 500 mm). An opening (width 150 mm, height 500 mm) on one of the box's sides allowed access to the testing apparatus. A black cloth curtain fastened to this side of the box was lowered before testing began. A window (width 150 mm, height 200 mm) cut out of the curtain was used for observing the spider, and the window also allowed some light into the box. During testing, the ambient light level at the Petri dish was approximately 10 cd/m^2 (International Light IL 1400 radiometer in integrated mode).

All testing was carried out between 0800 and 1200 h (laboratory photoperiod 12L:12D, lights on 0700 h). We never used an individual spider more than once in any experiment as a test spider or as a source spider. For standardization, all test and source spiders were unmated adults that had matured 2–3 weeks before testing. The distribution of post-maturation times for each treatment was roughly the same. No spiders had any direct contact with other individuals of either *Cyrba* species before or during testing. For standardizing hunger level, all test and source spiders were kept without food for 4–5 days before testing. We used chi-square tests of independence for comparing data from different experiments (null hypothesis: findings in one experiment same as in another experiment).

RESULTS

Olfactory tests.—As no male spiders from either *Cyrba* species displayed when the odor source was from a conspecific male or a heterospecific female, data from these tests were pooled. When the odor source was a conspecific female, we observed displaying in 24% of the trials in which the test spiders were *C. algerina* and in 32% of the trials when the test spiders were *C. ocellata*. Quiver-swim-waving alone was seen in 50% and 37.5% of the instances of displaying by *C. algerina* and *C. ocellata* males, respectively. In the remaining instances, we saw quiver-swim-waving in conjunction with other display behavior (*C. algerina* – 33.3% postured without dancing, 16.7% twitched their abdomens; *C. ocellata* – 25% twitched their abdomens, 25% twitched their abdomens and also postured, 12.5% postured without dancing and also while they danced).

When the odor sources were the draglines of conspecific females, 12% of the test spiders of both species displayed. Of the test spiders that displayed, 33% of these individuals quiver-swim-waved only, 33% also postured and 33% also twitched their abdomens.

Significantly more males displayed when the odor came from a conspecific female or a conspecific female's draglines instead of from a heterospecific female or a conspecific male (*C. algerina* – odor of a conspecific female, $X^2 = 13.04$, $P < 0.001$; odor of a conspecific female's draglines, $X^2 = 6.25$, $P < 0.05$; *C. ocellata* – odor of a conspecific female, $X^2 = 17.91$, $P < 0.001$; odor of a conspecific female's draglines, $X^2 = 6.25$, $P < 0.05$; Table 1). Although odor from conspecific females elicited display more often than odor from conspecific females' draglines, the difference was not significant for either *C. algerina* ($X^2 = 1.22$, $P = 0.269$) or *C. ocellata* ($X^2 = 2.91$, $P = 0.081$).

Tactile tests.—As no male spiders displayed when the draglines were from conspecific males or heterospecific females, we pooled data from these tests. However, when the draglines used came from conspecific females, most *Cyrba* males displayed (*C. algerina*: 72% of tests; *C. ocellata*: 88% of tests). Significantly more test spiders displayed in tactile tests when the draglines were from conspecific females instead of heterospecific females or conspecific males (*C. algerina*, $X^2 = 47.37$, $P < 0.001$; *C. ocellata*, $X^2 = 62.26$, $P < 0.001$).

Quiver-swim-waving alone was seen in 66.7% and 50% of the instances of displaying by *C. algerina* and *C. ocellata*, respectively. In the remaining instances, we observed quiver-swim-waving in conjunction with other display behavior

(*C. algerina* – 11.1% postured without dancing, 11.1% twitched their abdomens, 11.1% twitched their abdomens and also postured without dancing; *C. ocellata* – 27.3% postured without dancing, 13.6% twitched their abdomens, 4.6% postured without dancing and also while they danced, 4.6% twitched their abdomens and also postured without dancing and while they danced).

Olfactory-tactile tests.—When the odor chamber housed a conspecific female and there were draglines of a heterospecific female in the Petri dish, *C. algerina* and *C. ocellata* males displayed in 64% and 76% of the tests, respectively. Quiver-swim-waving alone was seen in 56.3% and 63.2% of the instances of displaying by *C. algerina* and *C. ocellata* males, respectively. In the remaining instances, quiver-swim-waving was seen in conjunction with other display behavior (*C. algerina* – 12.5% postured without dancing, 12.5% twitched their abdomens, 12.5% twitched their abdomens and also postured without dancing, 6.2% twitched their abdomens, postured without dancing and also while they danced; *C. ocellata* – 10.5% postured without dancing, 15.8% twitched their abdomens, 5.3% postured without dancing and also while they danced, 5.3% twitched their abdomens, postured without dancing and while they danced).

Comparisons.—When cues came from conspecific females, significantly more *Cyrba* males displayed during tactile tests than during olfactory tests (for olfactory tests, we pooled data from tests in which the odor source was a spider in the odor chamber with data from tests in which the odor source in the odor chamber was only the spider's draglines; *C. algerina*, $X^2 = 21.09$, $P < 0.001$; *C. ocellata*, $X^2 = 29.46$, $P < 0.001$).

The number of *Cyrba* males that displayed in olfactory-tactile tests (i.e., tests in which males could touch a heterospecific female's draglines while in the presence of the odor from a conspecific female) was significantly higher than the number of males that displayed during olfactory tests (i.e., tests in which a conspecific female spider was the odor source in the odor chamber and there were no draglines from another spider in the Petri dish) (*C. algerina*, $X^2 = 8.12$, $P < 0.05$; *C. ocellata*, $X^2 = 9.74$, $P < 0.05$).

Significantly more *Cyrba* males displayed in olfactory-tactile tests than in tactile tests in which the draglines they could touch came from heterospecific females (*C. algerina*, $X^2 = 23.53$, $P < 0.001$; *C. ocellata*, $X^2 = 30.65$, $P < 0.001$). However, the number of males that displayed during tactile tests in which the draglines came from conspecific females was not significantly different from the number that displayed during olfactory-tactile tests (*C. algerina*, $X^2 = 0.37$, $P = 0.544$; *C. ocellata*, $X^2 = 1.22$, $P = 0.269$).

DISCUSSION

Male *C. algerina* and *C. ocellata* initiated courtship when placed in a Petri dish in which a conspecific female had been present, but not when a heterospecific female or a conspecific male had been present. This type of evidence is commonly used for concluding that conspecific female draglines carry chemotactile pheromones and that these pheromones elicit male courtship behavior. If the tactile trials had been the only trials we carried out, we might have overlooked how tactile trials did not actually rule out olfaction. However, the fact that *Cyrba* males also displayed when they could not touch the draglines, but could detect the odor of draglines, suggests that female draglines also carry olfactory pheromones, and that these alone can elicit vision-based display behavior.

Knowing that the draglines of conspecific females are a source of olfactory pheromones, regardless of whether they are also a source of chemotactile pheromones, makes the outcome of taetile testing on its own more difficult to interpret. Our findings show that significantly more males initiated courtship during tactile tests than during olfactory tests. One possible explanation for this result is that tactile tests provided *Cyrba* males with two chemical-cue types (chemotactile and olfactory) instead of a single one (olfactory) and that the additive effects from these two kinds of chemical stimulation caused responses to be more frequent when draglines were present in the Petri dish.

However, results from olfactory-tactile tests suggest a different hypothesis. In these trials, the male was exposed to the odor of a conspecific female while in the presence of draglines from a female heterospecific. On their own, heterospecific female draglines did not elicit display during olfactory or tactile testing, suggesting that chemical cues from heterospecific females are not relevant to the male's display decisions. Yet the number of males that initiated vision-based display behavior in olfactory-tactile tests when using heterospecific female draglines was similar to the number of males that displayed during tactile tests using conspecific female draglines, and significantly higher than in olfactory tests when conspecific females were used as the odor source.

Hence, results from olfactory-taetile testing suggest that detecting purely tactile stimuli by touching draglines can increase a male's inclination to initiate courtship even when these are draglines from heterospecific females. It should be noted, however, that the heterospecific females used in our experiments were congeneric with the male test spiders and as such our experiments do not rule out an alternative hypothesis. Males might detect the pheromones present on the draglines of heterospecifc females, but these heterospecific pheromones might not suffice as courtship-eliciting stimuli; rather, they may have an additive effect when combined with the pheromones from a conspecific female in the odor chamber.

More experimental work is needed that aims at determining the actual origin of the pheromones generally attributed to draglines. Typically the salticid is left with blotting paper on which to deposit draglines. As draglines seem to be the dominant deposit left by spiders, it is convenient to attribute the results of these experiments to dragline-associated pheromones, but it is important to rule out the possibility that other deposits (e.g., feces) provide pheromone sources. Another possibility is that the blotting paper becomes impregnated with olfactory pheromones from the female spider's body and that these pheromones might also influence the test spider's behavior during tactile tests.

Although the males of 30 salticid species are known to be attracted to the odor of conspecifie females in olfactometer experiments (Nelson et al. 2012), adoption of vision-based courtship in response to female conspecific chemical signals has only been shown for three of them, *C. algerina* and *C. ocellata* in the present study and *E. culicivora* in an earlier study (Cross & Jackson 2013). However, in addition to vision-based

displays, many salticids, including *C. algerina* and *C. ocellata*, are also known to adopt a non-visual mode of courtship during encounters at nests or webs under dim light. Experiments have shown that, even in the absence of a resident female, contact with nest or web silk from conspecific females elicits male non-visual courtship behavior (Jackson 1987; Jackson & Pollard 1997). However, species from the genus *Cyrba* may be inclined to capture prey (Guseinov et al. 2004; Cerveira & Jackson 2011) and display under dim light to an extent that is unusual for salticids (Cerveira & Jackson unpublished data). An unusual level of activity under dim light might make olfactory pheromones that alert males to the presence of unseen prospective mates unusually important.

We are currently investigating a hypothesis, which, if confirmed, would be an example of males using a mate-locating tactic similar to a predatory tactic ('speculative hunting'; see Curio 1976) adopted by another salticid, *Portia fimbriata* (Doleschall 1859). In the presence of a particular prey odor, *P. fimbriata* is known to make undirected leaps. This behavior stimulates the prey to orient toward the leaping predator, revealing its location (Clark et al. 2000). We propose that, by initiating visible courtship after detecting pheromones in the absence of a visible target, *Cyrba* males solicit a response (i.e., displaying or becoming more active) by a not-yet-seen female, thereby making the female more easily seen by the male.

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LITERATURE CITED

Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton, New Jersey.

Barth, F.G. 2001. A Spider's World: Senses and Behavior. Springer, Berlin.

Bradbury, J.W. & S.L. Vehrenchamp. 2011. Principles of Animal Communication. Second edition. Sinauer Associates, Sunderland, Massachusetts.

Cardé, R.T. & J.G. Millar. 2004. Advances in Insect Chemical Ecology. Cambridge University Press, Cambridge, UK.

Carducci, J.P. & E.M. Jakob. 2000. Rearing environment affects behaviour of jumping spiders. Animal Behaviour 59:39–46.

Cerveira, A.M. & R.R. Jackson. 2011. Interpopulation variation in kairomone use by *Cyrba algerina*, an araneophagic jumping spider from Portugal. Journal of Ethology 29:121–129.

Cerveira, A.M. & R.R. Jackson. 2013. Love is in the air: olfaction-based mate-odour identification by jumping spiders from the genus *Cyrba*. Journal of Ethology 31:29–34.

Clark, R.J., D.P. Harland & R.R. Jackson. 2000. Speculative hunting by an araneophagic salticid spider. Behaviour 137:1601–1612.

Cross, F.R. & R.R. Jackson. 2013. The functioning of species-specific olfactory pheromones in the biology of a mosquito-eating jumping spider from East Africa. Journal of Insect Behavior 26:131–148.

Curio, E. 1976. The Ethology of Predation. Springer, New York.

Dumpert, K. 1978. Spider odor receptors: electrophysiological proof. Experientia (Basel) 34:754–756.

Ehn, R.H. & H. Tichy. 1996. Response characteristics of a spider warm cell: temperature sensitivities and structural properties. Journal of Comparative Physiology A 178:537–542.

Elias, D.O., S. Sivalinghem, A.C. Mason, M.C.B. Andrade & M. Kasumovi. 2010. Vibratory communication in the jumping spider *Phidippus clarus*: substrate-borne courtship signals are important for male mating success. Ethology 116:990–998.

Foelix, R.F. 1970. Chemosensitive hairs in spiders. Journal of Morphology 132:313–334.

Foelix, R.F. 2011. Biology of Spiders. Third edition. Oxford University Press, Oxford, UK.

Foelix, R.F. & I.-W. Chu-Wang. 1973. The morphology of spider sensilla. II. Chemoreceptors. Tissue and Cell 5:461–478.

Gaskett, A.C. 2007. Spider sex pheromones: emission, reception, structures, and functions. Biological Reviews 82:27–48.

Guseinov, E.F., A.M. Cerveira & R.R. Jackson. 2004. The predatory strategy, natural diet, and life cycle of *Cyrba algerina*, an araneophagic jumping spider (Salticidae: Spartaeinae) from Azerbaijan. New Zealand Journal of Zoology 31:291–303.

Harland, D.P., D. Li & R.R. Jackson. 2012. How jumping spiders see the world. Pp. 133–164. *In* How Animals See the World: Comparative Behavior, Biology, and Evolution of Vision. (O. Lazareva, T. Shimizu & E.A. Wasserman, eds.). Oxford University Press, New York.

Harris, D.J. & P.J. Mill. 1973. The ultrastructure of chemoreceptor sensilla in *Ciniflo similis* (Araneida, Arachnida). Tissue and Cell 5:679–689.

Jackson, R.R. 1987. Comparative study of releaser pheromones associated with the silk of jumping spiders (Araneae, Salticidae). New Zealand Journal of Zoology 14:1–10.

Jackson, R.R. 1990. Predatory versatility and intraspecific interactions of *Cyrba algerina* and *C. ocellata*, web-invading spartaeine jumping spiders (Araneae, Salticidae). New Zealand Journal of Zoology 17:157–168.

Jackson, R.R. & F.R. Cross. 2011. Olfactory sex and species discrimination by *Portia*, a genus of araneophagic jumping spiders. Journal of Arachnology 39:439–443.

Jackson, R.R. & S.E.A. Hallas. 1986. Predatory versatility and intraspecific interactions of spartaeine jumping spiders (Araneae: Salticidae): *Brettus adonis*, *B. cingulatus*, *Cyrba algerina* and *Phaeacius* sp. indet. New Zealand Journal of Zoology 13:491–520.

Jackson, R.R. & S.D. Pollard. 1997. Jumping spider mating strategies: sex among cannibals in and out of webs. Pp. 340–351. *In* Mating Systems in Insects and Arachnids. (J.C. Choe & B.J. Crespi, eds.). Cambridge University Press, Cambridge, UK.

Jiao, X., Z. Chen, H. Du, J. Chen & F. Lu. 2011. Chemoreceptor distribution and relative importance of male forelegs and palps in intersexual chemical communication of the wolf spider *Pardosa astrigera*. Chemoecology 21:45–49.

Land, M.F. & D.E. Nilsson. 2002. Animal Eyes. Oxford University Press, Oxford, UK.

Nelson, X.J., C.M. Warui & R.R. Jackson. 2012. Widespread reliance on olfactory sex and species identification by Lyssomanine and Spartaeine jumping spiders. Biological Journal of the Linnaean Society 107:664–677.

Schulz, S. 2013. Spider pheromones – a structural perspective. Journal of Chemical Ecology 39:1–14.

Shorey, H.H. 1976. Animal Communication by Pheromones. Academic Press, New York.

Steiger, S., T. Schmitt & H.M. Schaefer. 2011. The origin and dynamic evolution of chemical information transfer. Proceedings of the Royal Society B 278:970–979.

Symonds, M.R.E. & M.A. Elgar. 2008. The evolution of pheromone diversity. Trends in Ecology and Evolution 23:220–228.

Tichy, H., E. Gingl, R. Ehn, M. Papke & S. Schulz. 2001. Female sex pheromone of a wandering spider (*Cupeuius salei*): identification and sensory reception. Journal of Comparative Physiology A 187:75–78.

Trivers, R.L. 1972. Parental investment and sexual selection. Pp. 136–179. *In* Sexual selection and the descent of man. (B. Campbell, ed.). Aldine, Chicago.

Uhl, G. 2013. Spider olfaction: attracting, detecting, luring and avoiding. Pp. 141–157. *In* Spider Ecophysiology. (W. Nentwig, ed.). Springer, Berlin.

Willey, M.B. & R.R. Jackson. 1993. Olfactory cues from conspecifics inhibit the web-invasion behaviour of *Portia*, a web-invading, araneophagic jumping spider (Araneae, Salticidae). Canadian Journal of Zoology 71:1415–1420.

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Predatory response to changes in camouflage in a sexually dimorphic jumping spider

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Abstract. Cryptic animals tend to spend most of their lives keeping still. The majority of predators, however, including those cryptically colored, are forced to move in order to find and approach their prey. For such predators visibility may be an important factor influencing predatory behavior. Therefore we can expect differences in the way they approach their prey on backgrounds with different camouflaging properties. To test this, we examined the behavior of *Yllenus arenarius* Menge 1868 (Araneae: Salticidae), a cryptically colored jumping spider, hunting leafhoppers on backgrounds matching and non-matching for the spiders. Juvenile and female *Y. arenarius* are cryptic on light sand, but males lose their cryptic coloration for this background after their final molt. We designed an experiment to determine if increased visibility of the spiders influenced their predatory behavior. We found that background color had a significant effect on jumping distance, approaching speed and predatory success. On the light background cryptic spiders attacked from closer distances, approached prey with faster speeds and had higher success than on the dark background. Differences in approaching speed between males before and after final molt suggest a combined effect of background color and ontogenetic change of body coloration on the predatory decisions of these male spiders.

Keywords: Behavioral plasticity, crypsis, predatory behavior, salticid spider, *Yllenus arenarius*

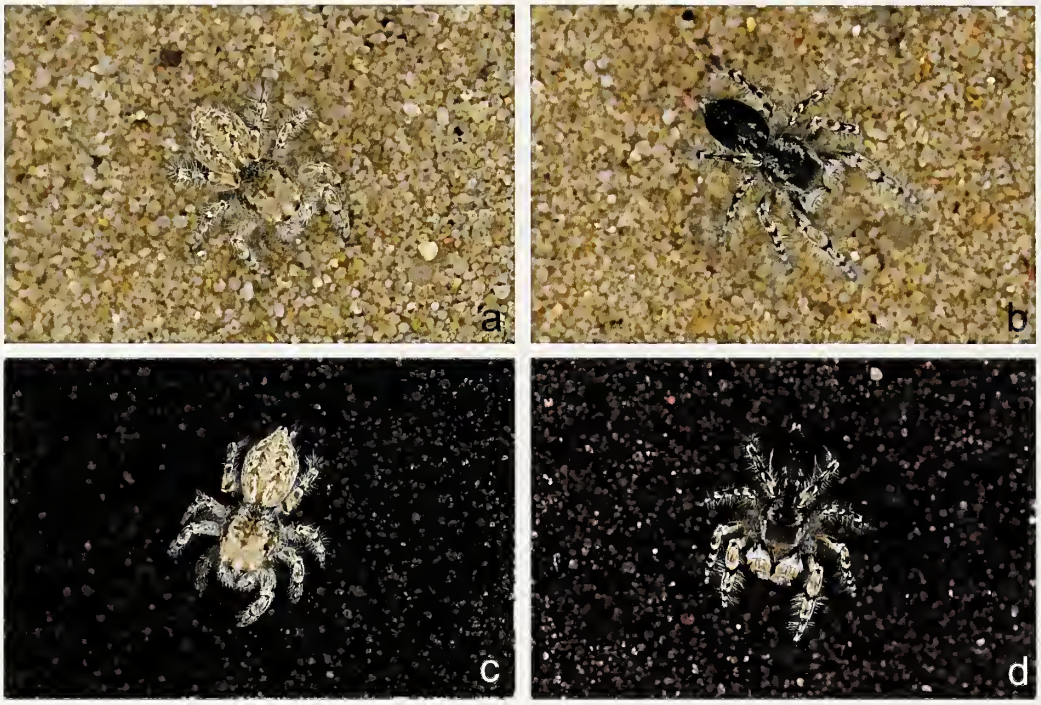
Crypsis is a common adaptation in the animal world (Cott 1957; Lima & Dill 1990; Ruxton et al. 2004). It decreases the risk of detection and recognition by other animals, which is crucial for the fitness of both prey and predator. However, this adaptation has only been well studied and described in detail for prey species (reviewed in Ruxton et al. 2004; Stevens 2007) and ambushing predators (Heiling et al. 2005; Chittka 2001; Théry & Casas 2002), while the role of cryptic coloration during active hunting has received very little attention (Bear & Hasson 1997). The general aim of this study was to examine the influence of this adaptation on the predatory behavior and hunting success of a cryptically colored spider.

One of the major differences between predators and prey, in terms of the risk of being detected, is their general mobility. Prey with a camouflaging adaptation tend to remain motionless, and when they must move from one place to another, they freeze as soon as they detect a predator (Broom & Ruxton 2005; Eilam 2005). Some predators use a similar mechanism to approach their prey. Sit-and-wait and ambush predators wait for their prey, keeping still until the prey is within striking distance (Curio 1976; Théry et al. 2005). Stalking predators tend to freeze when their prey stops moving and only continue their approach when the prey starts moving again and its ability to detect the predator is usually impaired (Schaller 1972; Harland & Jackson 2001). These results and other evidence suggest that background matching may not be effective at reducing the risk of detection when animals are in motion (Ioannou & Krause 2009). A number of cryptically colored predators cannot remain motionless as they have to search for prey and, when the prey is located, approach it. This leads to the question of the extent to which cryptic coloration is effective, not only in the moments when the predator remains still but also when the predator is in motion (e.g., during active hunting). The first objective of this study was to determine whether the hunting success of a cryptically colored jumping spider that stalks its prey is higher on camouflaging than on contrasting background.

Jumping spiders are known to modify their behavior in response to various cues in prey capture, in order to avoid being detected by their prey. They hunt differently when approaching dangerous prey (Harland & Jackson 2002), when the prey is facing them (Li et al. 2003), when the prey's ability to defend itself is impaired (Wilcox et al. 1996; Li & Jackson 2003) or when the prey can easily escape (Edwards & Jackson 1993; Bear & Hasson 1997; Bartos 2007). The second objective of this study was to determine whether the cryptically colored spider changes its behavior based on the camouflaging properties of the background.

Bear and Hasson (1997) conducted a study dealing with the influence of a spider's visibility on its predatory decisions. They found that *Plexippus paykulli* (Audouin 1826) changed its hunting behavior depending on its visibility to the prey and prey type. *Plexippus paykulli* approached maggots with higher velocities than adult flies and attacked maggots from shorter distances than flies. However, Bear & Hasson did not measure the predatory success of the spiders. In our study we explored similar questions using a different experimental setup. We used a highly cryptic jumping spider, *Yllenus arenarius* Menge 1868, and tested it with different types of living prey instead of dead prey. We also measured the predatory success of spiders on different backgrounds.

Many animals change their appearance during ontogeny, and some of them lose their cryptic coloration. A classic example of this process can be found in sexually dimorphic animals. Adult males and females of such animals may differ markedly in appearance, while immature individuals from both sexes closely resemble each other (Andersson 1994). Typically, females remain drab or cryptic after maturation, but males change their coloration and often become conspicuous, which can be a serious handicap in predator avoidance



Figures 1a–d.—Spiders and backgrounds used in the experiments. a, c. Adult female; b, d. Adult male; a, b. Light background; c, d. Dark background. Female in figures a and c is the same individual (note right leg 1 shorter in both figures). The male in figures b and d is also the same individual.

(Endler 1983; Magnhagen 1991; Zuk & Kolluru 1998). It is very likely that the loss of cryptic coloration may also affect hunting success; however, this issue has not been studied. The third objective of this study was to determine whether ontogenetic changes in a predator's conspicuousness are accompanied by corresponding changes in its decisions on how to hunt and in its hunting success.

METHODS

The predator.—We used *Yllenus arenarius*, a euryphagous jumping spider that stalks its prey, as the model for this study (Bartos 2007). This cryptically colored spider lives on the bare sandy dunes of the central and eastern Palearctic. There are two primary substrates with different camouflaging properties in the natural habitat of *Y. arenarius*: light, loose sand and dark patches of sand covered by a matt of lichens and algae. Light sand occurs in the majority of open areas, especially in the interior of the dune. Dark sand is a rare substrate that occurs on the outskirts of the dune. It appears as a result of primary succession of light sand. Light sand is a camouflaging background for females throughout their lives and for males until their final molt. The colors and patterns of these spiders closely match those of the sand, and if the spiders do not move they are very difficult to detect (Fig. 1). Dark sand often creates a patchwork with areas of light sand, and has camouflaging properties for adult males, but not for females and subadult males.

This spider is long lived. It has the longest reported lifespan among jumping spiders (Bartos 2005) and for the majority of its life cycle, 15 months from hatching (including six months of its first winter hibernation), males remain light in color and their coloration is indistinguishable from female coloration (M. Bartos personal observation). Only after their final molt do males develop secondary sexual traits, and for approximately the last 9.5 months of their lives (including six months of their second winter hibernation) they are brown with grey-brown annulations on their pedipalps and legs.

In our experiments we used *Y. arenarius* from two age groups: shortly before their final molt and shortly after their final molt. Spiders in the first group, referred to as subadults, were collected from early to mid-July, shortly before their final molt when they were 14–15 months old. Spiders in the second group, referred to as adults, were collected from mid-August to mid-September, shortly after their final molt when they were 15–16 months old. Based on previous field observations, we knew that these spiders hatch and molt synchronously. Using a method developed in past experiments, we could precisely estimate the spiders' ages on the basis of their phenology, size and maturity (Bartos 2005). Before the final molt we used pedipalp development to determine the sex of an individual. Male pedipalps become swollen a few weeks before their final molt thus enabling reliable sex determination. After the final molt we determined sex on the basis of the spider's general appearance. Light-colored females (subadult and adult) and subadult males were referred to as light spiders throughout these experiments due to their light coloration. Adult males, which are dark brown in color, were referred to as dark spiders (Fig. 1).

We collected all spiders from a dune in central Poland (Kwilno, 51°59′N, 19°30′E). In order to reduce the influence of laboratory conditions on the behavior of *Y. arearius* we carried out the experiments the same day or the day after we collected the specimens. Before the experiments we kept the spiders individually in glass containers (10 cm height, 10 cm by 10 cm width) with a layer of dune sand on the bottom. We released the spiders into the field after completing the

experiments. To avoid using the same spiders more than once we released them in areas isolated by dense vegetation from where we collected spiders for experiments later in the season.

The prey.—We chose small (3–4 mm body length), light grey leafhoppers *Psammotettix sp.* (Hemiptera: Cicadellidae), as the prey species in our experiments. This species moves unwillingly, but has a high escape potential (M. Bartos personal observation) due to its strong jumping legs (Burrows 2007). These leafhoppers are common in the natural diet of *Y. arenarius* (Bartos 2011). In earlier studies of *Y. arenarius*, it was observed that the spider uses prey-specific hunting behavior for catching this leafhopper (Bartos 2007, 2008). We collected leafhoppers in the field by sweep-netting dune grass on the day of the experiment or the day before and held them individually in plastic tubes. In order to reduce mortality of the prey, we stored them in a refrigerator at 5°C and took them out 15 min before the experiment started. Each prey item offered to a spider was within the size range of 60% ± 10% of the spider's body length, which is the prey size preferred by *Y. arenarius* (Bartos 2011). We measured the body length of prey and spiders with a stereomicroscope and a measuring ocular. We chose each prey item randomly for the experiments.

General methods.—We carried out the experiments within a white cardboard arena (15 cm high by 20 cm diameter) with a 1-cm-thick sand layer on the bottom. We used two types of background: a) light natural sand (camouflaging for light spiders), and b) dark sand, which was the natural sand dyed dark brown (camouflaging only for adult males) (Fig. 1). We dyed sand with a brown food dye that is non-toxic for spiders and their prey.

In the experiments we visually judged spider camouflage. Some insects and jumping spiders are, however, sensitive to UV light (Yamashita & Tateda 1976; Peaslee & Wilson 1989; Briscoe & Chittka 2001), which is not perceived by the human eye. Jumping spiders may also be dimorphic under UV (Lim & Li 2006; Lim et al. 2007). In the laboratory we used only artificial light sources with very low intensity of UV light (incandescent bulb) or emitting UV-C in spectra not detected by insects and jumping spiders (Li et al. 2008) (fluorescent tube ceiling lights emitting UV waves around 254 nm). Furthermore, the spiders were tested on highly contrasting or matching backgrounds illuminated with a high intensity of visible light; therefore, it is unlikely that such a low intensity of UV light produced by the light sources could have a significant effect on the spiders' overall visibility.

In the experiments we had eight different sets of spiders: subadult males, subadult females, adult males, adult females tested on light background and subadult males, subadult females, adult males, adult females tested on dark background (Fig. 1). For the experiments we chose each spider randomly and used it only once in the tests. We first dropped a spider into the arena and after one min we dropped a prey item 8 cm from the spider. The prey and the spider were dropped through non-transparent plastic tubes. We left the prey with the spider for 15 min and recorded the interaction using a video camera placed above the arena. Sand surface was brushed between tests to remove draglines and after that the surface layer (about 5 mm thick) was removed. The arena was then refilled with new sand up to the previous level. All the experiments took place between 09:00 and 16:00 (laboratory light regime, 12L:12D, lights on at 08:00). Lighting was from a 100W PILA incandescent bulb positioned 0.5 m above the arena and by fluorescent tube ceiling lights 2 m above the arena.

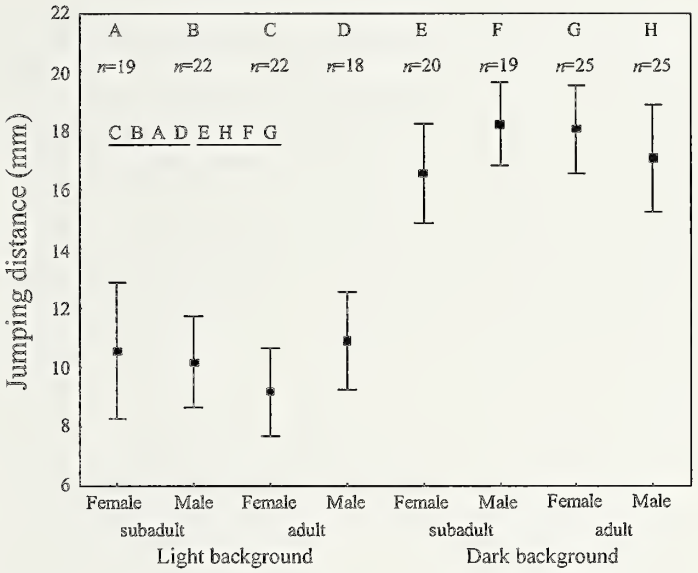


Figure 2.—Jumping distance of subadult and adult males and females of *Yllenus arenarius* on leafhoppers (*Psammotettix sp.*) on light and dark backgrounds. Central points are means, whiskers are ±1.96SE.

We recorded hunting success and measured jumping distance and approaching speed for each encounter. Distances and velocities were measured in Corel Draw 9.0 with a millimeter scale recorded together with the hunting sequence. Measurements were made in screen captures. Velocities were calculated based on the distance measurements and camera recording speed (25 frames per second). Because spiders decelerated while approaching their prey and jumping distance was different on different backgrounds, we always measured the approaching speed a fixed distance from the point of the spider's jump (5–15mm). Since subadult and adult spiders are of similar size (Bartos 2005), we directly compared their jumping distances and approaching speeds without any correction for size changes due to molt. Moreover, there was no difference in distances and velocities between the age groups except for the changes connected with the loss of camouflage in males (subadult versus adult males on light and dark backgrounds) (Figs. 2, 3). We only used measurements from the trials during which the prey did not move, because the spiders' behavior (especially approaching speed) depends on the prey's behavior (if prey moves more quickly, the spider approaches more quickly) (M. Bartos unpublished results). The majority of leafhoppers remained motionless after dropping into the arena; therefore, the trials in which the prey moved during spider approach constituted less than 20% of initial data in each of eight testing groups. From the tests on the light background we used 19 of 23 trials with subadult females, 22 of 26 with subadult males, 22 of 25 with adult females and 18 of 21 with adult males. From tests on the dark background we used 20 of 24 trials with subadult females, 19 of 23 with subadult males, 25 of 30 with adult females and 25 of 29 with adult males.

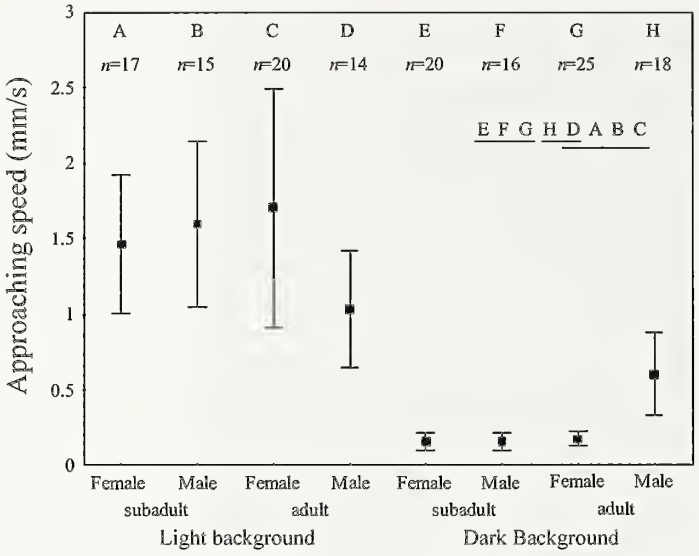


Figure 3.—Approaching speed of subadult and adult males and females of *Yllenus arenarius* on leafhoppers (*Psammotettix sp.*) on light and dark backgrounds. Central points are means, whiskers are ±1.96SE.

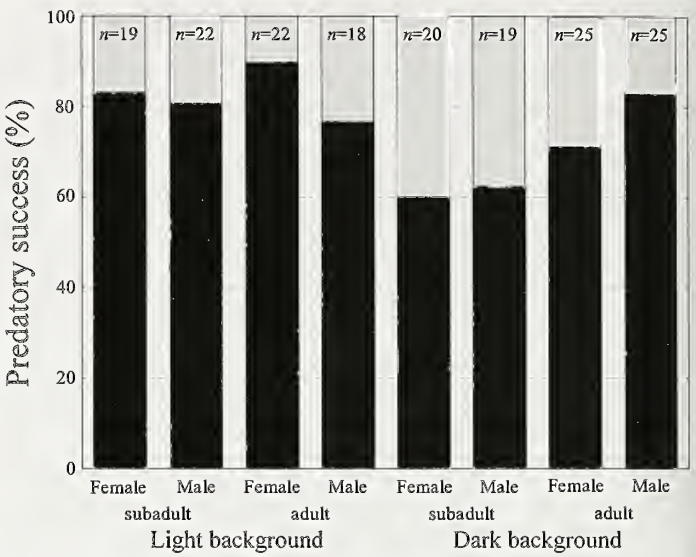


Figure 4.—Predatory success of subadult and adult males and females of *Yllenus arenarius* hunting leafhoppers (*Psammotettix sp.*) on light and dark backgrounds.

Voucher specimens of *Y. arenarius* were deposited in the Arachnological Collection of the Department of Zoology, University of Podlasie, Siedlce, Poland.

Data analysis.—We used general linear models to analyze the influence of background color, spider age and spider sex on jumping distance and approaching speed. All independent variables were used as categorical fixed factors. To reduce heteroscedasticity we applied a Box-Cox transformation on jumping distance and approaching speed. We performed post hoc comparisons using Tukey's unequal *n* HSD test. To analyze the influence of background color, spider age and spider sex on predatory success we used generalized linear models with binomial error and logit link functions. In the model we included single variables (background, sex, age) and the interaction among the three variables (background*sex* age). The significanee of particular independent effects was assessed with the Wald statistic (W). The stepwise procedures of backward removal were used to select for significant independent variables. We performed all analyses using Statistica 10 software (StatSoft, Inc.). Statistical procedures followed those described by Zar (1984).

RESULTS

Background color significantly affected jumping distance ($F = 148.95$, $df = 1$, $P < 0.0001$). On the light background all spiders moved closer to their prey before jumping than did spiders on the dark background (Fig. 2). These results occurred irrespective of the spiders' age, sex and the interaction of these factors.

Background color also influeneed approaching speed ($F = 161.62$, $df = 1$, $P < 0.0001$). Only spider sex and spider age were insignificant factors (Fig. 3). The interaction of background color, age and sex was, however, significant ($F = 6.38$, $df = 1$, $P < 0.02$). Spiders that hunted on the light background had significantly higher approaching speeds than those on the dark background. Differences between light spiders approaching on light and dark background were highly significant (Tukey's unequal n HSD: all $P < 0.0001$). However, the speed of approach of adult males on different backgrounds did not differ. The mean speed of adult males was, however, about 30% lower than that of subadult males (and other spiders) on the light background. More data for adult males might change the results. Adult (dark) males approaehed more quickly on the dark background than light spiders (Tukey's unequal n HSD: all $P < 0.01$), but slower than light spiders on light backgrounds (Tukey's unequal n HSD: all $P < 0.01$).

Background color significantly affected predatory success (W = 4.06, $df = 1$, $P < 0.05$). Spider sex, spider age and the interaction of these factors did not affect success (Fig. 4). Spiders hunting on a light background had higher predatory success than those on a dark background. These findings appear to result from the differences between light-colored spiders on light and dark backgrounds, as dark-colored males had the lowest success of all spiders on the light background and the highest success of all spiders on the dark background.

DISCUSSION

Our results provide evidence that *Y. arenarius* adapts its predatory behavior to matching properties of the background. In our experiments, spiders from all tested groups approached their prey differently on light and dark backgrounds. The differences concerned two aspeets of predation: the distance from which the prey was attacked and the speed at which the prey was approached. These differenees suggest that the spiders perceived changes in their own visibility on different backgrounds and the associated risk of being detected, which is consistent with the results obtained in different experimental conditions by Bear and Hasson (1997) using a stalking salticid. Similar findings have also been observed in ambushing salticids (Li et al. 2003).

The spiders' decisions about the distance of attack and the approaching speed may also be related to the risk of the prey's spontaneous departure. Different background colors can influence the length of time the prey spends in a given area

(reviewed by Lima & Dill 1990). As we used light-colored prey, for which dark sand was non-matching, we can expect a higher probability of the prey leaving in comparison to the background on which the prey was less visible. We did not quantify the risk of prey escape on different backgrounds; however, such a phenomenon has been reported for numerous prey species (reviewed by Lima & Dill 1990). It is unlikely that spiders reacted directly to differences in a prey's behavior on different backgrounds rather than to the color of the backgrounds, because in our analyses we used only those recordings in which prey did not move. For this reason, spiders were unlikely to perceive any prey behavior that could be a sign of preparation for escape. In addition, all prey were captured on the ground, which suggests that they were captured before they tried to escape.

Our findings provide evidence that background matching can be effective when animals are in motion. The movement of a cryptically colored animal certainly reduces the efficacy of its protective coloration, but background matching can still be functional, particularly if the receiver is poor-sighted. In our experiments such a conclusion is suggested by the higher predatory success of light spiders on light rather than dark backgrounds. The higher success rate may be attributed to two factors: a) lower conspicuousness of a predator approaching its prey, which may result in fewer instances of prey escape and b) a shorter attack distance, which allows for a more precise strike and a firmer grasp of the prey. The second factor is a direct consequence of the first, since a closer approach is likely to occur when detection risk decreases (Bear & Hasson 1997). Hence, both reasons for higher success lead to the conclusion that a spider on a light background was less visible to the prey during its movement.

The behavior of *Y. arenarius* hunting its prey can be better understood if we consider the different types of risks it faces during approach and the most likely causes of failure, such as: a) early detection by the prey before the strike, b) the prey's escape after the strike, c) the prey's spontaneous departure (prey leaves without perceiving the danger) or d) interference by competitors or the spider's own enemies (Bear & Hasson 1997). The analysis of all the potential risks reveals numerous trade-offs between contradictory decisions, each of which is associated with a different payoff (Bear & Hasson 1997). It is possible that the light spiders on a light background approached their prey more rapidly because the risk of detection was lower and because the risk of a prey's spontaneous departure and the risk of interference by other predators were minimized. Light spiders attacked on a light background from a shorter distance than on a dark background, again possibly because the cryptic coloration reduced their risk of detection and because it increased the precision of their strike.

The behavior of adult males on light and dark backgrounds needs to be discussed separately, as some aspects of their approach seem to be different from the predicted ones. They attacked from the same distances as light spiders; that is, from a shorter distance on light background, where they were conspicuous, and a longer distance on a dark background, where they were cryptic. It may seem that this result contradicts the conclusions that concern trade-offs minimizing different types of risk. However, there are other likely explanations for such a behavior.

First of all, the change of a male's coloration after its final molt may not influence its predatory decisions. Contrary to this supposition, their behavior changed in another aspect of approach we tested (adult males approached faster on dark background than did light spiders). Also, an adult male's appearance may be neither as cryptic on the dark background nor as conspicuous on the light background as initially assumed. Adult males possess light pedipalps that may function as camouflaging shields, behind which they can hide some part of their darker body parts. They also possess light annulations on their legs and light lines surrounding their dark cephalothorax and abdomen. Their coloration seems to be a compromise toward camouflage on light and dark backgrounds that naturally occur in the spider's environment. This could, at least partially, explain why they had a similar hunting success on both experimental backgrounds and why they approached the prey with similar speeds.

The change in males' speed of approach on dark background after maturation was noticeable, which clearly suggests that they reacted not only to background color, but also to the effect of their own changed color. The final molt made them more conspicuous on the light background, where they had been cryptic only a few weeks before. Our study shows for the first time for a jumping spider, and, as far as we know, for any stalking predator, the combined effect of background color and ontogenetic changes in body coloration on predatory decisions.

Activity of males in the field after their final molt suggests that they are behaviorally pre-programmed for this change in coloration. During the limited time between their final molt and the time of the experiments males had little opportunity to gain experience on dark background because during that period they occupied inner, light areas of the dune. They climbed higher spots, which they guarded against other males, and from there they visually searched for females. Thus, it is unlikely that a male's ability to adapt its approach to changes in its visibility after the final molt results from its experience in hunting on different backgrounds.

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LITERATURE CITED

Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton, New Jersey.

Bartos, M. 2005. The life history of *Yllenus arenarius* (Araneae, Salticidae) – evidence for sympatric populations isolated by the year of maturation. Journal of Arachnology 33:222–229.

Bartos, M. 2007. Hunting prey with different escape potentials – alternative predatory tactics in a dune-dwelling salticid. Journal of Arachnology 35:499–509.

Bartos, M. 2008. Alternative predatory tactics in a juvenile jumping spider. Journal of Arachnology 36:300–305.

Bartos, M. 2011. Partial dietary separation between coexisting cohorts of *Yllenus arenarius* (Araneae: Salticidae). Journal of Arachnology 39:230–235.

Bear, A. & O. Hasson. 1997. The predatory response of a stalking spider, *Plexippus paykulli*, to camouflage and prey type. Animal Behaviour 54:993–998.

Briscoe, A.D. & L. Chittka. 2001. The evolution of color vision in insects. Annual Revue of Entomology 46:471–510.

Broom, M. & G.D. Ruxton. 2005. You can run—or you can hide: optimal strategies for cryptic prey against pursuit predators. Behavioral Ecology 16:534–540.

Burrows, M. 2007. Kinematics of jumping in leafhopper insects (Hemiptera, Auchenorrhyncha, Cicadellidae). Journal of Experimental Biology 210:3579–3589.

Chittka, L. 2001. Camouflage of predatory crab spiders on flowers and the colour perception of bees (Arachnida: Thomisidae/ Hymenoptera: Apidae). Entomologia Generalis 25:181–187.

Cott, H.B. 1957. Adaptive Coloration in Animals. Methuen & Co., London.

Curio, E. 1976. The Ethology of Predation. Springer-Verlag, Berlin.

Edwards, G.B. & R.R. Jackson. 1993. Use of prey-specific predatory behaviour by North American jumping spiders (Araneae, Salticidae) of the genus *Phidippus*. Journal of Zoology 229:709–716.

Eilam, D. 2005. Die hard: a blend of freezing and fleeing as a dynamic defense—implications for the control of defensive behaviour. Neuroscience & Biobehavioral Reviews 29:1181–1191.

Endler, J.A. 1983. Natural and sexual selection on color patterns in poeciliid fishes. Environmental Biology of Fishes 9:173–190.

Harland, D. & R.R. Jackson. 2001. Prey elassification by *Portia fimbriata*, a salticid spider that specializes at preying on other salticids: species that elicit cryptic stalking. Journal of Zoology 255:445–460.

Harland, D.P. & R.R. Jackson. 2002. Influence of cues from the anterior medial eyes of virtual prey on *Portia fimbriata*, an araneophagic jumping spider. Journal of Experimental Biology 205:1861–1868.

Heiling, A., K. Cheng, L. Chittka, A. Goeth & M.E. Herberstein. 2005. The role of UV in crab spider signals: effects on perception by prey and predators. Journal of Experimental Biology 208: 3925–3931.

Ioannou, C.C. & J. Krause. 2009. Interactions between background matching and motion during visual detection can explain why cryptic animals keep still. Biological Letters 5:191–193.

Li, D. & R.R. Jackson. 2003. A predator's preference for egg-carrying prey: a novel cost of parental care. Behavioral Ecology and Sociobiology 55:129–136.

Li, D., R.R. Jackson & M.L.M. Lim. 2003. Influence of background and prey orientation on an ambushing predator's decisions. Behaviour 140:739–764.

Li, J., M.L.M. Lim, Z. Zhang, Q. Liu, F. Liu, J. Chen & D. Li. 2008. Sexual dichromatism and male colour morph in ultraviolet-B reflectance in two populations of the jumping spider *Phintella vittata* (Araneae: Salticidae) from tropical China. Biological Journal of the Linnean Society 94:7–20.

Lim, M.L.M. & D. Li. 2006. Extreme ultraviolet sexual dimorphism in jumping spiders (Araneae: Salticidae). Biological Journal of the Linnean Society 89:397–406.

Lim, M.L.M., M.F. Land & D. Li. 2007. Sex-specific UV and fluorescence signals in jumping spiders. Science 315:481.

Lima, S.L. & L.M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Magnhagen, C. 1991. Predation risk as a cost of reproduction. Trends in Ecology and Evolution 6:183–185.

Peaslee, A.G. & G. Wilson. 1989. Spectral sensitivity in jumping spiders (Araneae, Salticidae). Journal of Comparative Physiology A 164:359–363.

Ruxton, G.D., T.N. Sherratt & M.P. Speed. 2004. Avoiding Attack: the Evolutionary Ecology of Crypsis, Warning Signals and Mimicry. Oxford University Press, Oxford.

Schaller, G.B. 1972. The Serengeti Lion. University of Chicago Press, Chicago.

Stevens, M. 2007. Predator perception and the interrelation between different forms of protective colouration. Proceedings of the Royal Society B 274:1457–1464.

Théry, M. & J. Casas. 2002. Predator and prey views of spider camouflage. Nature 415:133.

Théry, M., M. Debut, D. Gomez & J. Casas. 2005. Specific color sensitivities of prey and predator explain camouflage in different visual systems. Behavioral Ecology 16:25–29.

Wilcox, R.S., R.R. Jackson & K. Gentile. 1996. Spiderweb smokescreens: spider trickster uses background noise to mask stalking movements. Animal Behaviour 51:313–326.

Yamashita, S. & H. Tateda. 1976. Spectral sensitivities of jumping spider eyes. Journal of Comparative Physiology A 105:29–41.

Zar, J.H. 1984. Biostatistical Analysis. 2nd edition. Prentice-Hall, New Jersey.

Zuk, M. & G.R. Kolluru. 1998. Exploitation of sexual signals by predators and parasitoids. Quarterly Review of Biology 73: 415–438.

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A glimpse into the sexual biology of the "zygiellid" spider genus *Leviellus*

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Abstract. We investigated the mating biology of the previously unstudied central European spider *Leviellus thorelli* (Ausserer 1871) by staging laboratory mating trials using males and females of varying mating histories. Our aim was to seek common themes in sexual behaviors of the sexually size-monomorphic "zygiellid" spiders with their putatively close relatives, araneids and nephilids, which are relatively well studied with respect to sexual biology. We found *L. thorelli* mating biology to more closely resemble that of sexually size-monomorphic araneids than that of dimorphic nephilids. Unlike in nephilids with sexually conflicted adaptations, we found no evidence for genital damage or plugging in *Leviellus* Wunderlich 2004, although we found rare cases of half-eunuchs. We suggest that the mating system of *L. thorelli* spiders is determined by short female sexual attractiveness, reduced receptivity after mating and/or intensive mate guarding.

Keywords: Mating system, genital plugging, mate guarding, sexual-size dimorphism, eunuchs

Sexual conflict theory concerns the idea that males and females may have different goals in reproduction (Watson 1991; Chapman et al. 2003; Arnqvist & Rowe 2005). As a consequenee of intersexual conflict, various morphological, physiological and behavioral adaptations have evolved, such as complex genitalia, multiple sperm storage organs, toxicity of seminal fluids, sexual cannibalism, and mate guarding (Parker 1984; Austad 1984; Chapman et al. 1995; Kuntner et al. 2009a; Uhl et al. 2010). These adaptations along with other demographic and ecological factors shape the mating system of a species.

Among invertebrates, spiders represent an especially suitable clade for sexual selection research (Eberhard 2004). In spiders, the prevailing mating strategy may largely be determined by two morphological constraints: genital morphology and delayed female maturation. First, spiders are classified into entelegyne and haplogyne species (Austad 1984; Uhl 2000; Uhl et al. 2010; Kuntner et al. 2009a). Haplogyne species possess a single insemination duct connected to spermathecae exhibiting last-male sperm priority (Austad 1984; Uhl 2000; Uhl et al. 2010). Alternatively, the entelegyne spiders have separate insemination and fertilization ducts connected to spermathecae and overwhelmingly exhibit first-male sperm priority (Austad 1984; Uhl 2000; Uhl et al. 2010). As a consequence, males of many entelegyne species have evolved mechanisms to avoid or reduce sperm competition with rival males by pre- or post-copulatory mate guarding and by the production of mating plugs (reviewed in Uhl et al. 2010). Although these plugs are thought to largely prevent or delay subsequent mating, they are not universally effective even in closely related species, as studies on nephilid spiders have shown [contrast e.g., *Nephila pilipes* (Fabricius 1793), *Nephilengys malabarensis* (Walckenaer 1841) and *Herennia multipuncta* (Doleschall 1859)]: Fromhage et al. 2007; Schneider et al. 2008; Kuntner et al. 2009b; Kralj-Fišer et al. 2011). Besides mechanical plugging of stored sperm and mate guarding, males employ other mechanisms to reduce sperm competition. Such an example is chemical manipulation, where products of male genitalia that are transferred during copulation may induce female resistance for further matings or earlier oviposition (Eberhard 1997).

Further behavioral and physiological adaptations also shape the mating system of a given species. For example, in highly dimorphic species that produce mating plugs, the small males are often cannibalized after copulation (Nessler et al. 2009), either due to intersexual conflict (Arnqvist & Rowe 2005; Fromhage & Schneider 2005) or male sacrifice, which may have a selective advantage in increasing paternity (Elgar & Nash 1988; Andrade 1996; Elgar et al. 2000; Schneider et al. 2000) leading to monogynous mating systems. In some species, males are physiologieally limited to one mating (Downes 1978; Michalik et al. 2010) or females are receptive to only one mate (Alcock & Buchmann 1985).

Finally, female maturation in extremely sexually size dimorphic species is usually considerably delayed (Higgins 2000; Kuntner & Coddington 2009; Kuntner et al. 2009b). Along with ecological factors such as the duration of the reproductive season, the operational sex ratio, the female or male distribution and/or the travel costs to the mate (Riechert 1974, 1981; Fromhage et al. 2007, 2008), unsynchronized male and female maturation may substantially constrain an individual's copulation frequency.

Clade-wide comparisons in mating behavior are essential for revealing macroevolutionary patterns of mating strategies; however, some groups remain largely understudied. Here, we investigate a spider clade informally named "Zygiellidae", which contains temperate and subtropical representatives of several genera exhibiting a moderate sexual-size dimorphism, but diverse entelegyne genital morphologies (M. Gregorič unpublished data). Our ongoing phylogenetic work suggests a close association of the "Zygiellidae" group with the families Nephilidae and Araneidae. Within the former, sexual biology has been well studied in many genera. Many exhibit extreme sexual-size dimorphism and sexual cannibalism, where large females devour tiny males (Kralj-Fišer et al. 2011). In addition, males often engage in genital plugging, genital damage and mate guarding (Schneider et al. 2008; Kuntner et al. 2009a,b). In Araneidae, the sexual biology of most genera remains unstudied, but with some notable exceptions, e.g., *Argiope* (Audouin 1826) with similar sexual phenomena as

Figure 1.—Female (A) and male (B) of the monomorphic *Leviellus thorelli*. Scale bar = 5 mm.

found in Nephilidae (Fromhage et al. 2003; Foellmer & Fairbairn 2004; Zimmer et al. 2012).

To investigate differences and similarities among the three groups, we studied the sexual biology of a previously unstudied "zygiellid" *Leviellus thorelli* (Ausserer 1871) (Fig. 1). To determine whether the *L. thorelli* mating system is monogamous or polygamous, we collected female and male *L. thorelli* and tested them in staged mating experiments. We measured spider body size to estimate the levels of sexual size dimorphism (SSD), observed male-male competition and determined the occurrence of plugging, genital damage and sexual cannibalism.

METHODS

Study animals.—*Leviellus thorelli* spiders were collected in September and October 2009 on houses near Lukovica, central Slovenia (46°09′43″N, 14°41′30″E). We collected 64 adult spiders (33 females and 31 males) and kept them in the laboratory for behavioral trials. We placed the collected females into glass frames to allow them to build webs, whereas males were kept in foam-covered plastic vials. We watered and fed the spiders twice a week with *Drosophila* flies and mealworms and maintained a seasonal light-dark cycle (16:8).

Experimental protocol.—In staged mating experiments in the laboratory, we observed mating behavior and occurrences of remating with the same genital organ. Mating was staged by placing a male in the female web, approximately 10 cm away from her. We observed male and female pre-copulatory behavior (courtship), which palp (left/right/both) the male inserted, how long and how many times the male inserted each palp, which female copulatory opening (CO; left/right/both) he inserted into, whether the spiders were aggressive and how they behaved after copulation (e.g., mate guarding). Each observation lasted for two hours. After a trial, we gave a spider 1–12 days of rest before testing for remating.

To make inferences about the mating system, we conducted four types of experimental trials, depending on female and male mating history in the laboratory. We never staged a mating trial between a male and a female that had been previously tested together. In these trials we mated 1) both sexes with unknown mating history [n = 45 trials, n = 64 spiders (28 individuals that did not mate in their first trial were reused)], 2) previously copulated female and male with unknown mating history (female remating, n = 10 trials), 3) female with unknown mating history and a previously copulated male (male remating, n = 8 trials), and 4) both male and female previously copulated [female and male remating, n = 8 trials (2 males used in Experiment 3 were reused)]. When pairing already mated individuals, we devised pairs in such a way that the male could insert his virgin palp only into the female's used CO (insertions were always ipsilateral). For example, we paired a male with a virgin left palp and a used right palp with a female with a used left CO and a virgin right CO; hence, the virgin palp could be inserted only in the used CO and vice versa. If remating did not occur in two subsequent trials, we concluded that remating with the used genital organ was not possible.

In three trials we placed two males on a female's web to document male-male antagonistic behavior. At the end of all trials, the spiders were euthanized, fixed in 70% ethanol and examined morphologically. Voucher specimens are available from the authors.

Morphological examination.—We examined all specimens from mating trials for genital damage (n = 64) and measured their first tibia+patella lengths, carapace width and carapace length (n = 50) under a Leica MZ16 stereomicroscope. Following Kuntner & Coddington (2009), sexual-size dimorphism (SSD) is measured as the ratio of female to male body length (or any other size measure).

We macerated all palps in concentrated KOH overnight in order to make them transparent and expandable in distilled water. We excised and examined all epigyna externally, then macerated each epigynal preparation in concentrated KOH overnight, and carefully cleaned it with needles in distilled water (e.g., Kuntner et al. 2009b). This technique exposes the dorsal epigynal anatomy and renders spermathecae translucent, which allows any embolic leftovers lodged inside spermathecae to be seen under a stereomicroscope.

Statistical analyses.—We examined the difference in body size measures between the sexes using the Mann-Whitney U Test. Correlations between size measures were analyzed using the Pearson correlation. We used a Generalized Linear Mixed Model (GLMM) to test the effect of two fixed factors, male and female mating history in the laboratory (previously unmated in the laboratory, previously mated in the laboratory) and carapace length; and a random factor (individual code) on occurrence of copulation (yes, no). We sequentially deleted fixed terms in order of decreasing significance; only terms with $P \leq 0.1$ remained in the final model. We re-entered the excluded terms one by one into the final model to confirm that they did not explain a significant part of the variation. We ran all analyses in PASW Statistics 18 (Field 2005).

RESULTS

SSD.—Patella + tibia I, carapace width and carapace lengths were significantly correlated (patella + tibia I, carapace width: r = 0.63, n = 50, $P < 0.001$; patella + tibia I, carapace

length: $r = 0.62$, $n = 50$, $P < 0.001$; carapace width, carapace length $r = 0.71$, $n = 50$, $P < 0.001$). The sexes differed significantly in patella + tibia I length (Mann-Whitney U = 91, $P < 0.001$, $n = 50$) but not in carapace length and width (length: Mann-Whitney U = 254.5, $P = 0.264$, $n = 50$; width: Mann-Whitney U = 231.5, $P = 0.118$, $n = 50$). Using carapace length, SSD in *L. thorelli* was 1.29, which translates to a sexually-size monomorphic species (Kuntner & Coddington 2009).

Mating results.—In all staged mating experiments ($n = 71$), a male signaled a female by pulling or drumming on her web. Typically, he initially remained at the edge of the female's web where he attached silk, created a mating thread, plucked the threads of the female's web with his front legs and rubbed his palps. Eventually he walked on the mating thread toward the female resting in her retreat and sometimes touched her legs with his front legs. Then he retreated and rhythmically plucked and beat the mating thread with his front legs. The male repeated this sequence until the female emerged from her retreat, if receptive. During courtship, the female usually moved her first legs and palps and sometimes her abdomen, and turned toward the male. When (if) the female joined the male, they touched with legs in venter to venter position, then suddenly grasped each other with legs to form a ball-shaped outline (S1.—available online at http://www.bioone.org/doi/suppl/10.1636/Hi13-08). The male inserted one of his palps ipsilaterally. After approximately 7 min (mean ± SE, 6.82 ± 1.35 min, $n = 17$) the female and the male abruptly separated, the male usually hanging on the mating thread, and the female retreating (S1). Then, the female typically rubbed her copulatory openings with the third and fourth legs, whereas the male positioned himself approximately 3–5 cm away from the female, plucked the threads, and rubbed and cleaned his palps. A male always continued to court after copulation, but in no ease did the pair copulate again. In most trials, the female was not highly aggressive toward the male during or after copulation, and sexual cannibalism was only observed after one mating (5.9%). In some cases, however, the female and the male were aggressive to each other before the copulation, shaking the web and approaching each other with open chelicerae. In such cases, mating never ensued.

If two males were introduced into the same female web, they assumed an aggressive pose toward each other with front legs extended, shook the web, fought vigorously and chased and bit each other. In all three cases the larger male chased off the smaller one (S2.—available online at http://www.bioone.org/doi/suppl/10.1636/Hi13-08).

Of 71 mating trials (Fig. 2), copulation occurred in only 17 cases (23.9%). The occurrence of mating depended on male and female mating history ($F_{95.7,1} = 41.81$; $P < 0.001$). The male and the female copulated in 37.8% ($n = 45$) of the trials when both of them had not previously copulated in our experiments; however, we never observed spiders to copulate in experiments 2, 3 and 4. That is, spiders never remated and reused the genital organ they had previously used ($n = 26$ trials). The random effect was not significant.

Genital damage.—Two mated males ($n = 17$) emasculated one palp to become half-eunuchs (Kuntner et al. 2009b) after separating from the females they had copulated with. We found the damaged palps in the males' vials, implying that they were not stuck in the female genitalia during copulation but were rather self-removed after mating. Our morphological examination revealed no further damage to male pedipalps ($n = 31$) or any plug formation in female copulatory openings, ducts or spermathecae ($n = 33$).

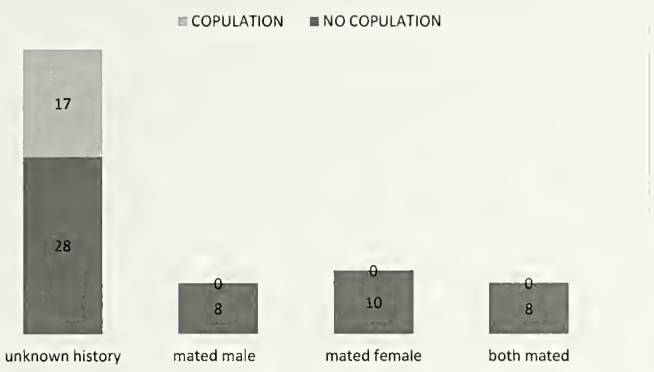

Figure 2.—Copulation success in four different combinations of female and male mating history in the laboratory. Unknown mating history = previously not mated in the lab.

DISCUSSION

One of our goals was to look for common themes in sexual behaviors of the sexual-size monomorphic "zygiellids" with their close relatives, araneids and nephilids. Copulation behavior of *Leviellus thorelli* resembles that of typical araneid species; males construct and court on a mating thread, with responsive females emerging out of the retreat and copulating with the male in a "hug posture" on the mating thread (Robinson 1982). Similar to other spiders with low levels of SSD, male *L. thorelli* apparently do not damage their genitals obligatorily and do not produce mating plugs, and females exhibit low levels of sexual cannibalism. We found little resemblance to nephilids, where extremely sexual-size dimorphic spiders engage in many ritualistic, sexually conflicted behaviors and strategies (Kuntner 2005, 2006, 2007; Schneider et al. 2005, 2008; Fromhage et al. 2007; Kuntner et al. 2009a, b; Zhang et al. 2011). However, laboratory and field observations of *L. thorelli* indicate intense mate guarding probably due to first-male sperm priority, where males should have reduced fitness benefits when mating with a previously mated female (Austad 1984). Yet, the question of the mating system in *L. thorelli*— and hence questions about macroevolutionary patterns in mating strategies among the three clades—remains open.

Among our aims was to determine the mating system in *L. thorelli*. A male or a female that had previously copulated in the laboratory was never observed remating, which could suggest that both sexes in *L. thorelli* might be either monogamous or at most bigamous. However, we acknowledge here a serious limitation of our study, precluding such definitive conclusion; we collected adult spiders from their natural setting with unknown mating histories, whereas to be conclusive, a study would better rear subadults to ensure virginity. Despite these limitations, the fact is that we never observed polygamy in *L. thorelli*, even though each individual was tested at least twice, with two different potential mates.

Hence, (extreme) polygamy seems unlikely in the system studied.

It is important to note that 60% of pairs failed to mate in the staged experiments. We presume that those spiders had mated before capture. If so, the females that received and stored enough sperm might bias their energy investment in egg production and fertilization, and hence might be sexually unreceptive. It is also likely that females were only receptive during molting and a short period thereafter (e.g., Alcock & Buchmann 1985; Gaskett 2007). Mated or older spider females can be aggressive and exhibit decreased receptivity to subsequent courting males (Elgar 1998), e.g., *Pholcus phalangioides* (Fuesslin 1775) (Schäfer & Uhl 2002), *Argiope keyserlingi* Karsch 1878 (Herberstein et al. 2002) and *Tegenaria atrica* C.L. Koch 1843 (Trabalon et al. 1997).

The alternative/additional explanation for the absence of remating is that males do not find the mated females sexually attractive, as is the case in *Tegenaria atrica* (Trabalon et al. 1997) and *Agelenopsis aperta* (Gertsch 1934) (Papke et al. 2001), both monogamous species that do not produce mating plugs. Male spiders in general prefer virgin over mated females, when females mate only once in several spiders; e.g., *Agelenopsis aperta* (Riechert & Singer 1995). It may vary among species whether a mated male or a female itself reduces female attractiveness. One or more such mechanisms might exist in *L. thorelli*, but this remains to be tested.

Based on our data, we cannot clarify why males did not remate (with the used palp) with a newly introduced female. Research on the closely related *Zygiella x-notata* indicates male choosiness for mates (Bel-Venner et al. 2008; Venner et al. 2010), where only 3% of guarding males switched to another female (Bel-Venner & Venner 2006). Although prolonged tandems during the reproductive season are known to reduce sperm competition and to lower sexual harassment of a mated female (Greenfield & Coffelt 1983; Schöfl & Taborsky 2002), it would be worth studying if and what mechanisms cause *L. thorelli* pairs to persist together in nature, or even to remain monogamous after separation. A phenomenon of prolonged tandems may relate to why no *L. thorelli* males use both palps during mating. In the field and laboratory, we observed that the male persists with the female for a long period with recurrent courting phases. Hence, it is possible that males use both palps with the same female, but over a longer episode than the observed two-hour trial in the laboratory.

Our results show no evidence for genital plugging, but we recorded two cases of male *L. thorelli* becoming eunuchs by severing their palps subsequent to mating. This resembles the eunuch behavior of *Hereuuia* Thorell 1877 (Kuntner 2005; Kuntner et al. 2009b), but not that of other nephilids where males leave a palp in the female genital tract (Kuntner et al. 2009c; Kralj-Fišer et al. 2011; Li et al. 2012), nor that of *Tidarren* Chamberlin & Ivie 1934 where the single-palped male spontaneously dies while copulating and thus functions as a whole-body mating plug (Knoflach & van Harten 2001). Although the eunuch's behavior in *Leviellus* is clearly not obligate, it may nevertheless be suggestive of some level of post-mating sterility in males.

In conclusion, *L. thorelli* sexual biology resembles that of araneids with low SSD and not that of nephilids, which exhibit pronounced SSD. Although our data require further corroboration with lab-reared spiders, they suggest that the mating system of *L. thorelli* spiders is shaped by a short period of female sexual attractiveness and/or reduced receptivity after mating and intensive mate guarding.

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LITERATURE CITED

Alcock, J. & S.L. Buchmann. 1985. The significance of post-insemination display by male *Centris pallida* (Hymenoptera, Anthophoridae). Zeitschrift für Tierpsychologie—Journal of Comparative Ethology 68:231–243.

Andrade, M.C.B. 1996. Sexual selection for male sacrifice in the Australian redback spider. Science 271:70–72.

Arnqvist, G. & L. Rowe. 2005. Sexual Conflict. Princeton University Press, Princeton, New Jersey.

Austad, S.N. 1984. Evolution of sperm priority patterns in spiders. Pp. 223–251. *In* Sperm Competition and the Evolution of Animal Mating Systems. (R.L. Smith, ed.). Academic Press, Orlando, Florida.

Bel-Venner, M.C., S. Dray, D. Allaine, F. Menu & S. Venner. 2008. Unexpected male choosiness for mates in a spider. Proceedings of the Royal Society B—Biological Sciences 275:77–82.

Bel-Venner, M.C. & S. Venner. 2006. Mate-guarding strategies and male competitive ability in an orb webspider: results from a field study. Animal Behaviour 71:1315–1322.

Chapman, T., G. Arnqvist, J. Bangham & L. Rowe. 2003. Sexual conflict. Trends in Ecology & Evolution 18:41–47.

Chapman, T., L.F. Liddle, J.M. Kalb, M.F. Wolfner & L. Partridge. 1995. Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland products. Nature 373:241–244.

Downes, J.A. 1978. Feeding and mating in insectivorous Ceratopogoninae (Diptera). Memoirs of the Entomological Society of Canada. Entomological Society of Canada, Ottawa, Ontario.

Eberhard, W.G. 1997. Sexual selection by cryptic female choice in insects and arachnids. Pp. 32–57. *In* The Evolution of Mating Systems in Insects and Arachnids. (J.C. Choe & B.J. Crespi, eds.). Cambridge University Press, Cambridge, UK.

Eberhard, W.G. 2004. Why study spider sex: Special traits of spiders facilitate studies of sperm competition and cryptic female choice. Journal of Arachnology 32:545–556.

Elgar, M.A. 1998. Sperm competition and sexual selection in spiders and other arachnids. Pp. 307–339. *In* Sperm Competition and Sexual Selection. (T.R. Birkhead & A.P. Möller, eds.). Academic Press, San Diego, California.

Elgar, M.A. & D.R. Nash. 1988. Sexual cannibalism in the garden spider *Araneus diadematus*. Animal Behaviour 36:1511–1517.

Elgar, M.A., J.M. Schneider & M.E. Herberstein. 2000. Female control of paternity in the sexually cannibalistic spider *Argiope keyserlingi*. Proceedings of the Royal Society of London Series B—Biological Sciences 267:2439–2443.

Field, A. (ed.). 2005. Discovering statistics using SPSS. Second edition. Sage Publications, London.

Foellmer, M.W. & D.J. Fairbairn. 2004. Males under attack: sexual cannibalism and its consequences for male morphology and behavior in an orb webspider. Evolutionary Ecology Research 6:163–181.

Fromhage, L., K. Jacobs & J.M. Schneider. 2007. Monogynous mating behaviour and its ecological basis in the golden orb spider *Nephila fenestrata*. Ethology 113:813–820.

Fromhage, L., J.M. McNamara & A.I. Houston. 2008. A model for the evolutionary maintenance of monogyny in spiders. Journal of Theoretical Biology 250:524–531.

Fromhage, L. & J.M. Schneider. 2005. Safer sex with feeding females: sexual conflict in a cannibalistic spider. Behavioral Ecology 16:377–382.

Fromhage, L., G. Uhl & J.M. Schneider. 2003. Fitness consequences of sexual cannibalism in female *Argiope bruennichi*. Behavioral Ecology and Sociobiology 55:60–64.

Gaskett, A.C. 2007. Spider sex pheromones: emission, reception, structures, and functions. Biological Reviews 82:27–48.

Greenfield, M.D. & J.A. Coffelt. 1983. Reproductive behaviour of the lesser waxmoth, *Achroia grisella* (Pyralidae: Galleriinae): signalling, pair formation, male interactions and mate guarding. Behaviour 84:287–315.

Herberstein, M.E., J.M. Schneider & M.A. Elgar. 2002. Costs of courtship and mating in a sexually cannibalistic orb-web spider: female mating strategies and their consequences for males. Behavioral Ecology and Sociobiology 51:440–446.

Higgins, L. 2000. The interaction of season length and development time alters size at maturity. Oecologia 122:51–59.

Knoflach, B. & A. van Harten. 2001. *Tidarren argo* sp. nov. (Araneae: Theridiidae) and its exceptional copulatory behaviour: emasculation, male palpal organ as a mating plug and sexual cannibalism. Journal of Zoology 254:449–459.

Kralj-Fišer, S., M. Gregorič, S. Zhang & M. Kuntner. 2011. Eunuchs are better fighters. Animal Behaviour 81:933–939.

Kuntner, M. 2005. A revision of *Heremia* (Araneae: Nephilidae: Nephilinae), the Australasian 'coin spiders'. Invertebrate Systematics 19:391–436.

Kuntner, M. 2006. Phylogenetic systematics of the Gondwanan nephilid spider lineage Clitaetrinae (Araneae, Nephilidae). Zoologica Scripta 35:19–62.

Kuntner, M. 2007. A monograph of *Nephilengys*, the pantropical 'hermit spiders' (Araneae, Nephilidae, Nephilinae). Systematic Entomology 32:95–135.

Kuntner, M. & J.A. Coddington. 2009. Discovery of the largest orbweaving spider species: The evolution of gigantism in *Nephila*. PLoS ONE 4(10):e7516.

Kuntner, M., J.A. Coddington & J.M. Schneider. 2009a. Intersexual arms race? Genital coevolution in nephilid spiders (Araneae, Nephilidae). Evolution 63:1451–1463.

Kuntner, M., S. Kralj-Fišer, J.M. Schneider & D. Li. 2009b. Mate plugging via genital mutilation in nephilid spiders: an evolutionary hypothesis. Journal of Zoology 277:257–266.

Kuntner, M., I. Agnarsson & M. Gregorič. 2009c. Nephilid spider eunuch phenomenon induced by female or rival male aggressiveness. Journal of Arachnology 37:266–271.

Li, D., J. Oh, S. Kralj-Fišer & M. Kuntner. 2012. Remote copulation: male adaptation to female cannibalism. Biology Letters 8:512–515.

Michalik, P., B. Knoflach, K. Thaler & G. Alberti. 2010. Live for the moment—Adaptations in the male genital system of a sexually cannibalistic spider (Theridiidae, Araneae). Tissue & Cell 42:32–36.

Nessler, S., G. Uhl & J.M. Schneider. 2009. Sexual cannibalism facilitates genital damage in *Argiope lobata* (Araneae: Araneidae). Behavioral Ecology and Sociobiology 63:355–362.

Papke, M.D., S.E. Riechert & S. Schulz. 2001. An airborne female pheromone associated with male attraction and courtship in a desert spider. Animal Behaviour 61:877–886.

Parker, G.A. 1984. Sperm competition and the evolution of animal mating strategies. Pp. 1–60. *In* Sperm Competition and the Evolution of Animal Mating Systems. (R.L. Smith, ed.). Academic Press, Orlando, Florida.

Riechert, S.E. 1974. Pattern of local web distribution in a desert spider—mechanisms and seasonal variation. Journal of Animal Ecology 43:733–746.

Riechert, S.E. 1981. The consequences of being territorial spiders, a case study. American Naturalist 117:871–892.

Riechert, S.E. & F.D. Singer. 1995. Investigation of potential male mate choice in a monogamous spider. Animal Behaviour 49:715–723.

Robinson, M.H. 1982. Courtship and mating behavior in spiders. Annual Review of Entomology 27:1–20.

Schäfer, M.A. & G. Uhl. 2002. Determinants of paternity success in the spider *Pholcus phalangioides* (Pholcidae: Araneae): the role of male and female mating behaviour. Behavioral Ecology and Sociobiology 51:368–377.

Schofl, G. & M. Taborsky. 2002. Prolonged tandem formation in firebugs (*Pyrrhocoris apterus*) serves mate guarding. Behavioral Ecology and Sociobiology 54:426–433.

Schneider, J.M., L. Fromhage & G. Uhl. 2005. Copulation patterns in the golden orb-web spider *Nephila madagascariensis*. Journal of Ethology 23:51–55.

Schneider, J.M., M.E. Herberstein, M.J. Bruce, M.M. Kasumovic, M.L. Thomas & M.A. Elgar. 2008. Male copulation frequency, sperm competition and genital damage in the golden orb-web spider (*Nephila plumipes*). Australian Journal of Zoology 56:233–238.

Schneider, J.M., M.E. Herberstein, F.C. De Crespigny, S. Ramamurthy & M.A. Elgar. 2000. Sperm competition and small size advantage for males of the golden orb-web spider *Nephila edulis*. Journal of Evolutionary Biology 13:939–946.

Trabalon, M., A.G. Bagnères & C. Roland. 1997. Contact sex signals in two sympatric spider species, *Tegenaria domestica* and *Tegenaria pagana*. Journal of Chemical Ecology 23:747–758.

Uhl, G. 2000. Female genital morphology and sperm priority patterns in spiders (Araneae). Pp. 145–156. *In* European Arachnology 2000. (S. Toft & N. Scharff, eds.). Aarhus University Press, Aarhus.

Uhl, G., S. Nessler & J. Schneider. 2010. Securing paternity in spiders? A review on occurrence and effects of mating plugs and male genital mutilation. Genetica 138:75–104.

Venner, S., C. Bernstein, M. Dray & M.C. Bel-Venner. 2010. Make love not war: When should less competitive males choose low quality but defendable females? American Naturalist 175:650–661.

Watson, P.J. 1991. Multiple paternity and first mate sperm precedence in the Sierra Dome spider, *Linyphia litigiosa* Keyserling (Linyphiidae). Animal Behaviour 41:135–148.

Zhang, S., M. Kuntner & D. Li. 2011. Mate binding: male adaptation to sexual conflict in the golden orb-web spider (Nephilidae: *Nephila pilipes*). Animal Behaviour 82:1299–1304.

Zimmer, S.M., K.W. Welke & J.M. Schneider. 2012. Determinants of natural mating success in the cannibalistic orb-web spider *Argiope bruennichi*. PLoS One 7:e31389.

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SHORT COMMUNICATION

Scavenging behavior in spitting spiders, *Scytodes* (Araneae: Scytodidae)

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Abstract. Spitting spiders, *Scytodes* spp., rapidly expectorate a zig-zag of silk from cephalothoracic glands through openings at the base of their fangs, tacking down prey before feeding. Previously, scavenging of dead prey was considered rare among the Araneae but, in laboratory bioassays, it is exhibited across a wide spectrum of spiders including *Scytodes* Latreille 1804. When presented with dead spiders as prey, two species of araneophagic *Scytodes* spiders secured their meals without deploying the probably metabolically expensive cephalothoracic silk in 25 of 30 feeding episodes. *Scytodes globula* Nicolet 1849 scavenged without spitting in 16 of 30 trials (53%), whereas *S. atlacoya* Rheims et al. 2007 did so in 9 of 36 trials (25%). Therefore, spitting spiders show behavioral plasticity in securing prey, conserving resources when necessary.

Keywords: Prey capture, behavioral plasticity, predation

Spiders of the genus *Scytodes* Latreille 1804 are unique among the Araneae in that they have enlarged cephalothoracic glands modified to produce a sticky silk-like substance that is rapidly expelled from openings at the base of their fangs, immobilizing prey by tacking it down to the substrate (Nentwig 1985; Li et al. 1999). The spider then bites the prey and wraps it loosely in spinneret silk before consuming it. A comprehensive analysis of the biomechanical features of spitting behavior in *S. thoracica* (Latreille 1802) is presented by Suter & Stratton (2009, 2013). Although *Scytodes* spiders do accept a wide variety of soft-bodied arthropods in the laboratory and in the field, they are preferentially araneophages (Li et al. 1999).

Scavenging in spiders has been occasionally researched in the last decade (Sandidge 2003; Cramer 2008; Vetter 2011). Regarding captive specimens and dead prey, Gabriel (2013) presents an interesting discussion of the use of thawed rodent carcasses to maintain the theraphosid *Sericopelma* Ausserer 1875, as well as suggestions for feeding mammalian organ meats to small spiderlings when providing live prey is logistically difficult. Vetter (2011) showed that a wide variety of spider taxa (one of which was a spitting spider, probably *S. fusca* Walckenaer 1837) were capable of scavenging dead crickets in the laboratory.

In general, venom is considered costly to produce, such that it is differentially metered out through venom optimization in several predators (e.g., snakes, spiders) (Wigger et al. 2002; Morgenstern & King 2013). For example, the amount of venom dispensed by the ctenid spider *Cupiennius salei* (Keyserling 1877) is correlated with prey escape intensity (Boevé 1994; Malli et al. 1999). Likewise, silk is considered metabolically costly, as evidenced by orb weavers recycling their webs and ingesting the silk after an episode of hunting (Peakall 1971). Thus, considering that scavenging behavior was documented in at least one spitting spider (Vetter 2011), the question arises as to whether spitting spiders exhibit differential use of their mucilaginous cephalothoracic silk. I predicted that *Scytodes* spiders would not waste their metabolically expensive silk when encountering dead arthropods.

Six specimens (one male, five females) of *Scytodes atlacoya* Rheims et al. 2007 and five specimens (one male, two females, two subadults) of *S. globula* Nicolet 1849 were collected around Athens, Georgia, in August 2012 and March 2013. The spiders were maintained in plastic vials of differing size, correlating with each spider's size. Voucher specimens are deposited at the California Academy of Sciences.

I tested the spiders individually in glass petri dishes (21 mm deep by 90 mm diameter) with glass lids. All petri dishes were placed on a sheet of aluminum foil, allowing the zig-zag of spit silk to be more readily observed. Due to the nocturnal nature of spitting spiders, tests were conducted in early morning where room lights were kept off during most of the behavioral observations. Subdued illumination of 27 to 36 lux over the field of foil from a light in an adjacent hallway provided ample illumination for observation. When more lighting was needed, room lights (700 lux) were turned on briefly to make observations of the spit silk. This sudden increase in illumination did not appear to startle or elicit a change in behavior of the predators, which were mostly slow moving or immobile throughout the experiment. Petri dishes were washed with hot water and detergent after each trial.

In initial tests to verify prey acceptability, I placed a live juvenile *Metaltella simoni* (Keyserling 1878) (Amphinectidae) into a petri dish with each spitting spider. The *M. simoni* spider was typically 70% to 100% of the body length of the spitting spider, collected from leaf litter in Riverside, California and used within one week of capture. In a preliminary trial, each of the eleven experimental *Scytodes* spiders accepted live *M. simoni* as prey and used their unique zig-zag spitting of cephalothoracic silk for capture, which was readily evident when viewed through the glass (Fig. 1). In other studies using similar sized prey, *Scytodes* spiders always spit silk to subdue prey (R. Suter personal communication).

For the scavenging tests, I collected *M. simoni* spiders and froze them overnight. The next day, they were thawed for 30 minutes in their vials to minimize water loss through desiccation, which can negatively affect prey suitability (Pollard 1989). I then introduced spitting spiders individually into the glass petri dishes. I placed a dead *M. simoni* spider of 50% to 120% of the predator's body size, approximately 1 cm in front of the spitting spider's cephalothorax, but not touching its legs, and then covered the petri dishes with glass lids. The placement of the prey item enhanced the probability that the spider would encounter the prey (spitting spiders do not move much under these conditions or any conditions that I could determine even when I handled them during the day). When they move, they slowly walk around the petri dish, probing cautiously with their legs. If the spitting spider moved away from the prey prior to initial discovery, I repositioned the dead spider in the spitting spider's potential path. I watched continuously for 90 minutes to assess scavenging success; some spiders did not move for the entire observation period. After the bioassay, spiders that did not feed were returned to their maintenance vials and tested the following week with new prey. Spiders that fed were allowed to continue feeding until they separated from the prey spider several hours later, were returned to their vials, and were tested again in two weeks. No additional prey was offered between trials during the assays; two spiders did not feed for the six weeks of their

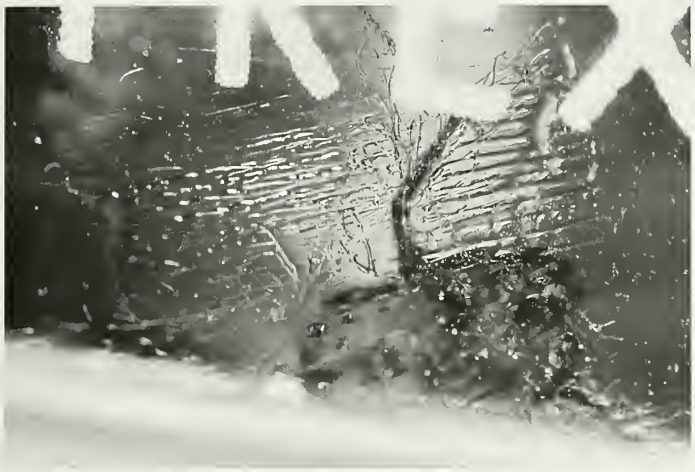

Figure 1.—The evenly spaced, parallel strands of cephalothoracic silk that were rapidly expectorated by a *Scytodes* spider, which immobilized a live, immature *Metaltella simoni* as seen through the glass wall of a petri dish.

portion of the experiment but nonetheless survived. Eleven spiders were offered dead prey six times each. Room temperature ranged from 17.9 to 22.3 C during testing.

The typical behavior prior to feeding on a dead *M. simoni* involved initial discovery where the spitting spider cautiously extended one of its first pair of legs in slow front-to-back sweeping exploratory movements, drawing its legs back toward the body. When the spitting spider sensed that there was something in its path, it once again cautiously extended its legs and probed. With additional sweeps and no response from the prey, the predator extended several legs, corralling the dead spider. The spitting spider then slowly drew the carcass toward its mouthparts, which were often not placed onto the prey for over a minute. Eventually, the mouthparts made contact with the dead spider, although whether this action involved a venom-delivering bite with fangs or the initiation of feeding behavior could not be determined. I allowed the spider a few minutes to secure its prey before I turned on room lights briefly to examine for cephalothoracic gland silk. In the initial cases, after a few minutes I carefully removed the glass lid to examine if the predator had spit silk on the prey and confirmed this by examining the petri dish under a microscope. This examination of the petri dish did not appear to disturb the spitting spider if handled gently. However, with experience, the microscopic confirmation was unnecessary.

Of the 66 trials, 30 (45%) resulted in feeding by *Scytodes* spiders. In 25 of these 30 trials with feeding (83%), the spitting spider did not use its unique cephalothoracic silk to secure the dead prey (Table 1). *Scytodes globula* scavenged without spitting in 16 of 18 feeding trials (89%) and in 53% of trials overall, whereas *S. atlacoya* scavenged without spitting in 9 of 12 feeding trials (75%) and 25% overall. This absence of spitting was evident in males, females and immatures with marked variation among them (Table 1). In one interesting trial, a *S. globula* female with an egg sac (the *Scytodes* female carries her egg sac in her fangs), approached the dead *M. simoni*, moved her egg sac behind her but still in contact with the abdomen and then started feeding without spitting. In the six trials involving spitting of silk, five *Scytodes* spiders fed and the other moved away without feeding. This latter case appeared to be defensive spitting elicited by the prey spider's movement caused by the *Scytodes* spider's probing leg rolling the carcass toward itself. In one case where the spider spit then fed, abdominal leakage was affixing the dead prey spider to the substrate; the predator spit during the struggle to detach the prey from the petri dish bottom. In some cases where no scavenging occurred, the spider was immobile, most likely attributable to satiation; several *Scytodes*

Table 1.—Results of scavenging by *Scytodes atlacoya* and *S. globula*. Each spider was tested six times for a total of 66 trials.

	Fed, no spit	Fed, spit	Spit, no feed	Did not feed
Scytodes atlacoya				
Male	3	1	0	2
Female #1	0	0	0	6
Female #2	1	0	0	5
Female #3	1	2	0	3
Female #4	0	0	1	5
Female #5	4	0	0	2
Total	9	3	1	23
Scytodes globula				
Male	2	0	0	4
Female #1	3	1	0	2
Female #2	5	0	0	1
Immature #1	3	1	0	2
Immature #2	3	0	0	3
Total	16	2	0	12
Total for both species	25	5	1	35

spiders had well-swollen abdomens during the trials. Similar to the closely related *Loxosceles* spiders, *Scytodes* spiders do not appear to need to eat frequently (i.e., once a month is sufficient to maintain them) (R. S. Vetter, pers. observation). Although the prey were dead, many of the spitting spiders still wrapped them in spinneret silk; this was probably to facilitate easier handling or, in nature, to prevent prey from slipping from their grip as the predators often carried the prey away in their fangs before eating.

Despite their small size and limited neurologic potential, spiders demonstrate feeding behavior that can be quite intricate and flexible, with extreme complexity exhibited by the well-known salticid spiders of the genus *Portia* Karsch 1878 (Nelson & Jackson 2011). Scavenging dead prey is probably a very rare natural event for spiders; however, they show behavioral plasticity if given the chance to do so. This opportunistic activity was exemplified in Vetter (2011), in which 99 of 100 spiders of diverse genera scavenged dead crickets in a laboratory study, including all 32 specimens of the web-spinning families Agelenidae, Amphinectidae and Filistatidae; the probability of these site-restricted web-spinners naturally encountering dead prey that they did not previously kill is virtually nil. Spitting spiders are able to assess prey status and usually conserve their probably metabolically expensive cephalothoracic silk when they encounter dead prey. Hence, when it comes to scavenging, *Scytodes* spiders typically don't give a spit.

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LITERATURE CITED

Boevé, J.-L. 1994. Injection of venom into an insect prey by the free hunting spider *Cupiennius salei* (Araneae, Ctenidae). Journal of Zoology London 234:165–175.

Cramer, K.L. 2008. Are brown recluse spiders, *Loxosceles rechusa* (Araneae, Sicariidae) scavengers? The influence of predator satiation, prey size, and prey quality. Journal of Arachnology 36:140–144.

Gabriel, R. 2013. Notes and observations regarding unusual feeding behaviour of a *Sericopelma* Ausserer, 1875 with comments on

carrion feeding and spiders leaving their burrows after heavy rains (Araneae: Theraphosidae). Newsletter of the British Arachnological Society 126:8–9.

Li, D., R.R. Jackson & A.T. Barrion. 1999. Parental and predatory behaviour of *Scytodes* sp., an araneophagic spitting spider (Araneae: Scytodidae) from the Phillipines. Journal of Zoology, London 247:293–310.

Malli, H., L. Kuhn-Nentwig, H. Imboden & W. Nentwig. 1999. Effects of size, motility and paralysation time of prey on the quantity of venom injected by the hunting spider *Cupiennius salei*. Journal of Experimental Biology 202:2083–2089.

Morgenstern, D. & G.F. King. 2013. The venom optimization hypothesis revisited. Toxicon 63:120–128.

Nelson, X. & R.R. Jackson. 2011. Flexibility in the foraging strategies of spiders. Pp. 31–56. *In* Spider Behaviour: Flexibility and Versatility. (M.E. Herberstein, ed.). Cambridge University Press, Cambridge, UK.

Nentwig, W. 1985. Feeding ecology of the tropical spitting spider *Scytodes longipes* (Araneae, Scytodidae). Oecologia (Berlin) 65:284–288.

Peakall, D.B. 1971. Conservation of web proteins in the spider, *Araneus diadematus*. Journal of Experimental Biology 176:257–264.

Pollard, S. 1989. Constraints affecting partial prey consumption by a crab spider, *Diaea* sp. indet. (Araneae: Thomisidae). Oecologia 81:392–396.

Sandidge, J. 2003. Scavenging by brown recluse spiders. Nature 426:30.

Suter, R.B. & G.E. Stratton. 2009. Spitting performance parameters and their biomechanical implications in the spitting spider, *Scytodes thoracica*. Journal of Insect Science 9:62.

Suter, R.B. & G.E. Stratton. 2013. Predation by spitting spiders: elaborate venom gland, intricate delivery system. Pp. 241–251. *In* Spider Ecophysiology. (W. Nentwig, ed.). Springer-Verlag, Berlin.

Vetter, R.S. 2011. Scavenging by spiders (Araneae) and its relationship to pest management of the brown recluse spider. Journal of Economic Entomology 104:986–989.

Wigger, E., L. Kuhn-Nentwig & W. Nentwig. 2002. The venom optimisation hypothesis: a spider injects large venom quantities only into difficult prey types. Toxicon 40:749–752.

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SHORT COMMUNICATION

Ant mimicry in the spider *Myrmecotypus iguazu* (Araneae: Corinnidae), with notes about myrmecomorphy in spiders

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Abstract. We describe the mimetic relationship between the ant-like spider *Myrmecotypus ignazu* Rubio & Arbino 2009 (Araneae: Corinnidae) and the carpenter ant *Camponotus sericeiventris* Guérin (Hymenoptera: Formicidae), studied in a subtropical rainforest in Iguazú National Park, Argentina. The morphological adaptations, aspects of coloration, and behavior responsible for the ant-like appearance in *M. ignazu* (the mimic) provide strong evidence that its model is *C. sericeiventris*. Both field observations and field and laboratory experiments suggest that this spider is a Batesian mimic.

Keywords: Ant-like spider, Batesian mimics, behavior, mimetic relationship, Paranaense rainforest

Spiders are generalist predators found in diverse environments. Because most of them are small, soft-bodied arthropods and lack defensive protection against larger predators, they can become prey of these predators, especially of those that use their vision to detect prey (such as wasps, birds, spiders, frogs, and small lizards). Many species of spiders have evolved adaptations that are thought to provide protection against such visually hunting predators.

Many spiders, particularly in the families Salticidae and Corinnidae, have evolved mimetic resemblance to ants, or myrmecomorphy (Simon 1897; Mello-Leitão 1939; Galiano 1965, 1966, 1967, 1969; Reiskind 1969, 1970, 1977; Cushing 1997, 2012). By means of myrmecomorphy, many spiders and insects resemble their models through behavioral and morphological convergence (McIver & Stonedahl 1993; Cushing 1997, 2012; Debandi & Roig-Juñent 1999). Many mimetic spiders have a constricted carapace that gives them a three-segment body appearance, and some have specialized setae on the carapace providing color patterns similar to those on the model ant's gaster. Moreover, numerous myrmecomorphic spiders lift the first pair of legs off the ground and carry out exploratory movements while contacting the substratum much like the antennal movement of ants (antennal illusion), and this behavior further increases the mimetic resemblance (McIver & Stonedahl 1993).

Most ants are unpalatable for generalist predators because they have efficient defense mechanisms, such as hard integument, sometimes with spines, strong mandibles, and stings connected to the poison gland, which expel irritating acid substances. Further, ants can act en masse to attack or defend the colony (Reiskind 1977; Oliveira 1988; Hölldobler & Wilson 1990; Cushing 1997, 2012; Joron 2003). Ants inhabit almost all terrestrial habitats and have few specialized predators. For this reason, ants constitute a stable model for Batesian mimics (Oliveira 1986). Myrmecomorphy is observed in 45 families of insects and in nine families of spiders (McIver & Stonedahl 1993; Cushing 1997).

Over 200 species of ant-mimicking spiders are presently known (Cushing 1997, 2012). The majority is found among salticids (e.g., *Myrmarachne, Synemosyna, Synageles, Belippo, Zuniga*), corinnids (e.g., *Castianeira, Myrmecinn, Myrmecotypus, Sphecotypus, Mazax*), gnaphosids (e.g., *Micaria*), thomisids (e.g., *Amyciaea, Aphantochilus*), and zodariids (e.g., *Zodarion, Storena*) (Reiskind 1969, 1977; Foelix 1996; Cushing 1997, 2012; Pekár & Kŕál 2002). However, studies on myrmecomorphy of spiders in Argentina are scanty. Galiano's (Galiano 1965, 1966, 1967, 1969, 1996) revisions of the "formiciformes" salticids cite the genera *Sarinda, Martella* and *Synemosyna* for Argentina as imitative species of ants. The purpose of this paper is to present ant mimicry in *Myrmecotypus iguazu* Rubio & Arbino 2009 and to describe the adaptations responsible for the ant-like appearance and behavior in the mimic, with evidence from field and laboratory observations, as well to discuss aspects of spider myrmecomorphy.

Specimens were collected in two localities of the Iguazú and General M. Belgrano Departments, Misiones Province, Argentina: Iguazú National Park (INP – 25.683333°S, 54.433333°W) and Urugua-í Wildlife Reserve (UWR – 25.974345°S, 54.116330°W). The environment consists of subtropical rainforests, which corresponds to the Paranaense phytogeographic region (Cabrera & Willink 1973). The annual temperature and annual precipitation vary between 16 and 22 °C, and 1000 and 2200 mm respectively (Placci & Di Bitetti 2006).

The study was carried out in both the field and laboratory. Spiders and ants were observed, photographed and sampled in January 2005 and January 2009. The specimens were captured during the day, mainly on the handrails of the different tourist circuits of the INP (Fig. 3G). In the laboratory, the experiments were conducted in January 2009 in the CIES (Centro de Investigaciones Ecológicas Subtropicales – INP). The aims of these experiments were 1) to describe the behaviors in the field, 2) to observe the general reactions of the model and mimic toward one another and 3) to test the hypothesis that the myrmecomorphs might be aggressive mimics. Aggressive mimics are species that use deceptive signaling (morphological and/or behavioral) to lure their own prey (Wickler 1968; Vane-Wright 1980). Examples of possible aggressive spider myrmecomorphs include *Aphantochilus* and *Strophius* (Thomisidae) that were observed in same sampling localities carrying ants in their chelicerae (Oliveira & Sazima 1984, 1985). The dead ant carried by the spider is hypothesized to provide chemical cues that serve to lure other ants close to the spider predator.

All experiments were carried out with adult specimens of the myrmecomorphic spider, *Myrmecotypus ignazu* (Corinnidae: Castianeirinae) and the proposed model, *Camponotus sericeiventris* (Formicidae: Formicinae). *Myrmecotypus iguazu* is known from the type

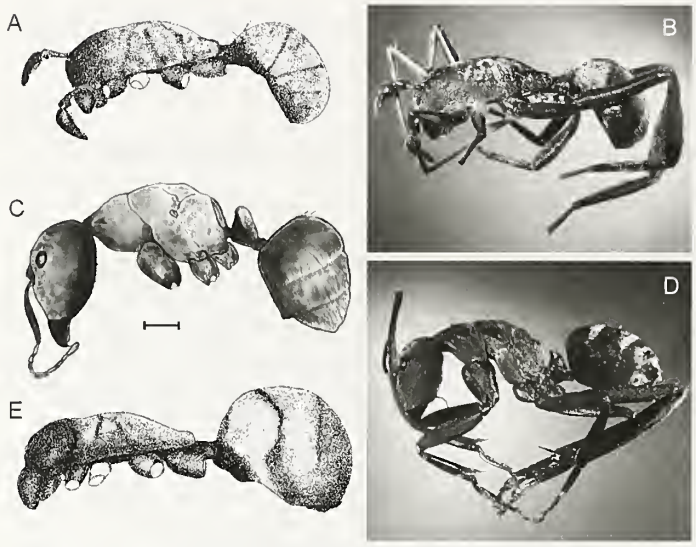

Figure 1.—Close resemblance between the mimetic spider *Myrmecotypus iguazu* (A, B: male; E: female) and its ant worker model *Camponotus sericeiventris* (C, D), lateral view. Note the lengthened carapace with slightly darker coloration in the anterior part simulating the head and thorax of ant, the transverse black bands in the spider's abdomen resembling the segmented gaster of the ant, and the similar pattern of golden reflective pubescence of both species (photos). Scale = 1 mm.

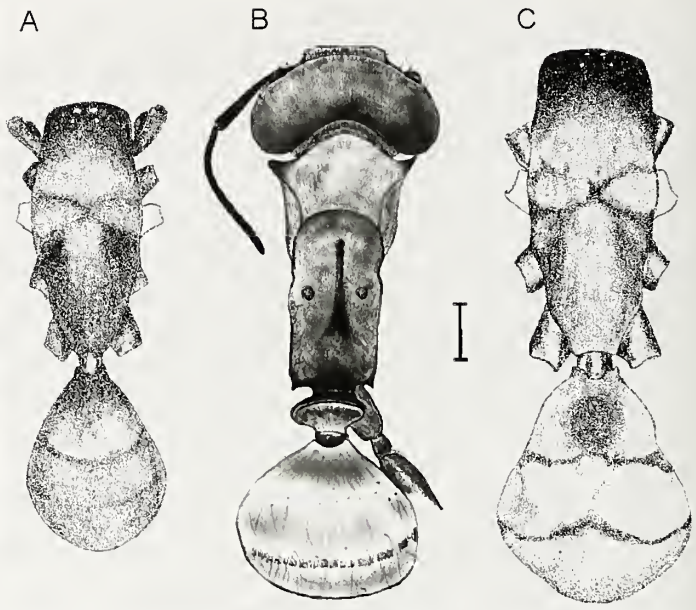

Figure 2.—Dorsal view of the mimetic spider *Myrmecotypus iguazu* (A: male; C: female) and its ant worker model *Camponotus sericeiventris* (B). Note the lengthened carapace with slightly darker coloration in the anterior part simulating the head and thorax of the ant, the transverse black bands in the spider's abdomen resembling the segmented gaster of ant, and the dorsal golden or silver reflective pubescence (whitened area in the drawing) of both species. Scale = 1 mm.

locality in INP and from UWR (Rubio & Arbino 2009). The ant *C. sericeiventris* is exclusively Neotropical and is subdivided into six subspecies (Wheeler 1931; Kempf 1972; ITIS 2013). In Argentina, *C. sericeiventris* is found in Chaco, Corrientes and Misiones provinces (Wheeler 1931; Cuezzo 1998), and according to Wheeler (1931) the subspecies to which we refer is *C. sericeiventris sericeiventris*, although of a slightly smaller size than that of the original description.

To test the hypothesis that *M. iguazu* is an aggressive mimic, one female or one male was placed inside a Petri dish (95 mm diameter) with a moistened piece of filter paper and a twig with leaves that could serve as the spider's retreat. Because there was little difference in size and overall appearance between male and female spiders, we used either one in the experiment. Three minor/median ant workers of *C. sericeiventris* were added to each dish with an adult (female or male) *M. iguazu*, and the behavior of the spider in the presence of multiple models was observed. For each encounter between spiders and ants, three replicates were carried out with observation sessions of 60 min for each one. We used a different set of ants for each trial. Three different females and three different males of *M. iguazu* were used. We performed 18 tests. Interactions between spiders and ants were also observed in the field. If *M. iguazu* is an aggressive mimic, we expected spiders to pursue ants in the Petri dishes. If the spider is a myrmecomorph but not an aggressive mimic, then we expected to see avoidance behaviors on the part of the spiders.

Selection for ant mimicry in spiders influences their behavior, habitat preference and morphology (McIver & Stonedahl 1993). In this analysis, certain morphological indices for mimicry were measured: comparing the values of *M. iguazu* with those of the myrmecomorphic species *Myrmecotypus rettenmeyeri* Unzicker 1965 (see Reiskind 1969), which also mimics the ant *C. sericeiventris*, and with a sympatric non-mimetic corinnid *Falconina gracilis* (Keyserling 1891). Reiskind (1970) indices can be used as indicators of mimicry and are derived by dividing the width by the length of the body segments (see below). Any elongation of structures (carapace, sternum or abdomen) will result in low index values. Ant-mimicking spiders should have low indices, since thinness and elongation of the overall body (cephalothorax and abdomen) often enhance the mimetic resemblance. The following indices were used: 1) carapace index = carapace width / carapace length × 100; 2) sternum index = sternum width / sternum length × 100 and 3) abdomen index = abdomen width / abdomen length × 100. The latter index is often particularly important in male myrmecomorphs whose abdomens are completely covered by sclerites, making this index less variable.

We used a Leica® MS5 stereoscopic microscope for photographs. Other photos of ants and spiders in their natural habitat were taken with a Nikon® D80 digital camera. All measurements were taken with a micrometric ocular micrometer and were recorded in millimeters. Voucher specimens of the species examined were deposited in the following institutions: Colección Nacional Aracnológica, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-Ar 19708, 19709); Museo de La Plata (MLP 17926); Colección Aracnológica de la Cátedra de Diversidad Animal I, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba (CDA 000.806 to 000.811); and Colección de Artrópodos de la Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste (CARTROUNNE 7818) (see Rubio & Arbino 2009).

Solitary male and female *M. iguazu* were found wandering among workers of *C. sericeiventris* (ratio of 5 spiders to 95 ants in a group of approximately 400 ants). The field observations supported a strong resemblance between the purported mimic and model in morphology, coloration, and behavior. It was very difficult to detect the spiders among the ants (Fig. 3F).

Morphological and coloration convergences.—Ant workers have opaque black bodies that are dimorphic in color, with 80% of individuals covered with a dense pubeseence of all golden setae and 20% covered with all silver setae over the alitrunk, petiole, coxae, and gaster (Figs. 1C, D; 2B; 3B, D). This notable golden or silver pubescence is completely reflective. The antennae are long and the third pair of legs longer than the rest (Fig. 3B, D). The workers are polymorphic (Wheeler 1931; Yamamoto & Del-Claro 2008); the

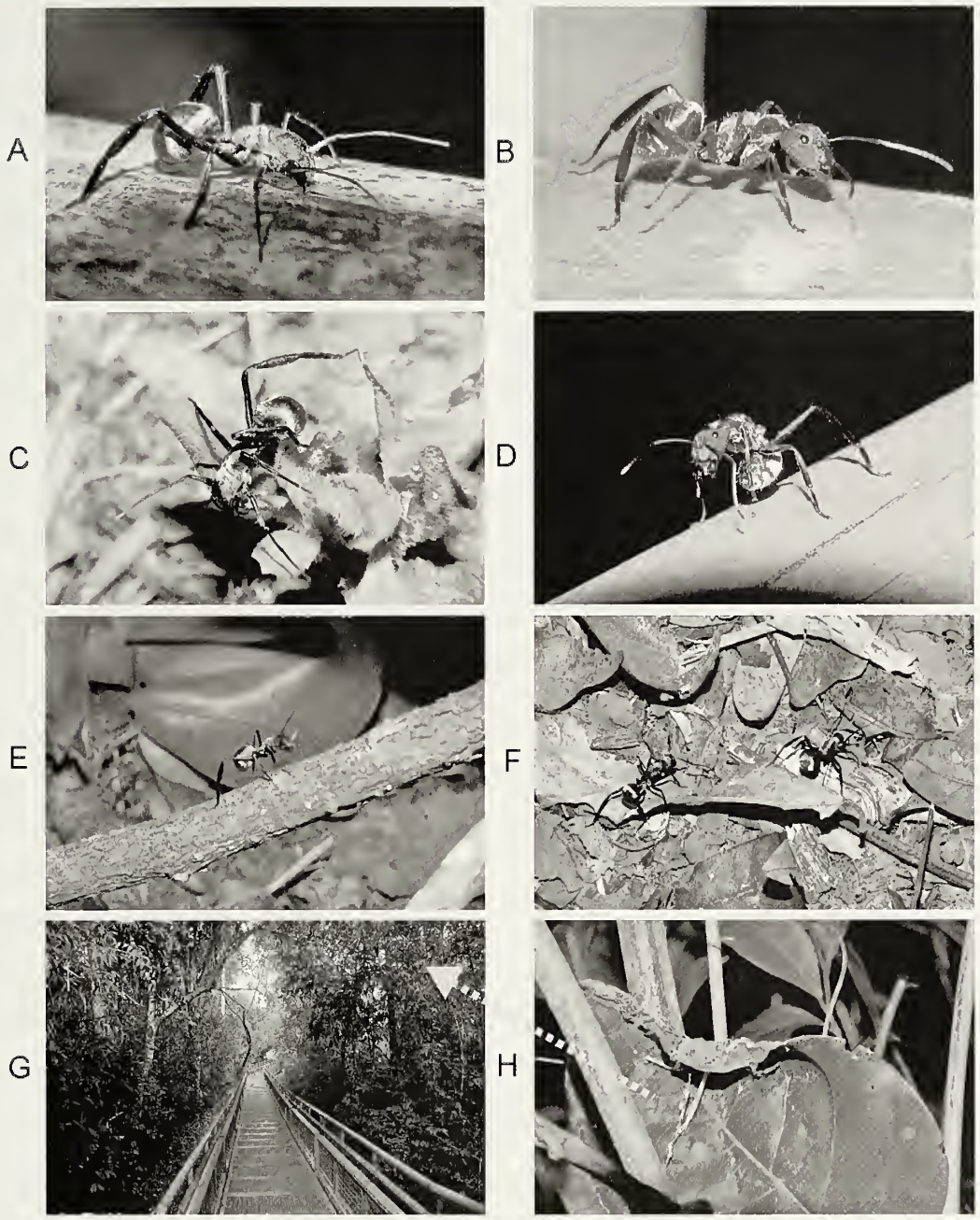

Figure 3.—Habitus and nature of the mimetic spider *Myrmecotypus iguazu* and its ant worker model *Camponotus sericeiventris* in Iguazu National Park, 2009 (A, C, E: female spiders; B, D: ant worker; F: both species wandering in a trail over the ground; G: habitat that the species inhabit; both spiders and ants wander the handrails of the paths together; H: spider refuge in a fold of a green leaf of the foliage, indicated by an arrow.

larger workers vary between 15–16 mm, and median and minor workers between 10–13 mm (Figs. 1C; 2B).

Morphological and color resemblances of female and male *M. iguazu* are evidenced in the lengthened carapace with a sinuous side view and narrow dorsum (Fig. 1A, B, E). A slight constriction in the anterior third, marked with a black line, gives the impression of a division of the cephalothorax into a cephalic region and a separate thoracic region, resulting in the three-segment appearance of body characteristic of ants (Fig. 1E). The head mimicry is emphasized by darker coloration in the anterior third of the carapace and by strong chelicerae resembling ant jaws. The abdomen is oval, with two faint thin transverse black bands shaped by different colors of hair; this aspect looks like the tergites of the ant abdomen (Figs. 1A, E; 2A, C). In addition, the resemblance is reinforced by the opaque black coloration of the body and by the reflective golden pubescence on the abdomen and posterior region of the carapace (Fig. 3A, C).

The largest females *M. iguazu* reach a total length of 9.7 mm and males 7.3 mm; relative leg lengths longest to shortest are IV-I-III-II, with the first pair much thinner than the others (Rubio & Arbino 2009) (Figs. 1B; 3A, C). Relative leg lengths in *C. sericeiventris* are III-II-I, the third pair corresponding to the fourth pair in spiders. The following morphological indices were mimicry indicators for *M. iguazu* (see Rubio & Arbino 2009), and values in parentheses were given by Reiskind (1969) for *M. rettenmeyeri*: Male: carapace index 43.4 (39); sternum index 46.2 (39); abdomen index 68.9 (66). Female: carapace index 42.1 (38–39); sternum index 37.7 (39–41); abdomen

index 78.7 (69–87). In comparison, the non-mimetic corinnid *Falconina gracilis* had the following indices: male carapace index 74.5, sternum index 87.9, and abdomen index 62.7; and female carapace index 87.2, sternum index 91.7 and abdomen index 62.1. The abdomen indices in *Myrmecotypus* species were high due to the globose abdomens of these mimics.

Behavioral mimicry.—*Myrmecotypus iguazu* wandered actively on the handrails of the paths together with workers of *C. sericeiventris*, moving quickly and stopping sporadically (Fig. 3A, E). The locomotion was always carried out with the first pairs of legs raised forward and moved with slight swinging movements, touching the substratum with the tip of the tarsus, simulating the ants' antennae (Fig. 3A, B, E). Moreover, the tip of the abdomen was slightly curved down, contacting the substratum with the spinnerets, as do ants with the gaster. When perturbed, the spiders adopted a posture comparable to ants facing a similar situation: spiders put the abdomen under the carapace, pointed forward (spray illusion), as the ants do when expelling formic acid (Fig. 3D).

As light levels decreased with approaching night the ants returned to their nests in the rainforest vegetation; the spiders ascended searching a refuge in the foliage, generally in a fold of a green leaf where they weave a retreat as do other corinnids (Fig. 3H). However, during twilight hours one female *M. iguazu* was observed walking alone on the ant trails, although the workers of *C. sericeiventris* had already moved to their nests.

Spiders and ants wandered together in the same places/trails, and encounters between the two seemed to be random. The laboratory experiments resulted in mutual avoidance in all 18 tests with the six spiders; each encounter of a spider with an ant resulted in a quick escape by both model and mimic, especially by the spider, which ran lengths of about 60 mm avoiding contact even before contact occurred. In a typical encounter, the spider walked away from the ant before resuming its movement around the dish. Similar avoidance behavior was observed in the field.

Myrmecotypus rettenmeyeri, a Panamanian spider that resembles *C. sericeiventris,* has this single species as its model (Reiskind 1969). Similarly, *M. iguazu* is an ecological equivalent of *M. rettenmeyeri*, whose males and females are specialized mimics of the same ant species, *C. sericeiventris* (Fig. 3A, B, F).

Support for mimicry.—The following characteristics were considered to demonstrate the existence of mimicry among the species studied (Reiskind 1977): 1) Sympatry: both spiders and ants are found in the same microhabitats of both localities and are found wandering together. 2) Similarity involves morphological and ethological aspects, and patterns of coloration. These aspects were remarkably similar between the species, as was shown in this study. 3) Species specificity: the mimic possesses some structures analogous to the model that are not present in related species of the same genus. The features that fulfill this criterion are the reflective pubescence over the carapace and abdomen of the spiders, and the golden coloration of this pubescence, similar in distribution to the workers of *C. sericeiventris*. However these characteristics are an "indirect proof" of myrmecomorphy according to Reiskind (1977).

Function of mimicry.—Most myrmecomorphic spiders are presumed to be Batesian mimics (Cushing 1997; Oliveira 1986, 1988; McIver & Stonedahl 1993; Reiskind 1977). *Myrmecotypus iguazu* were difficult to differentiate when they moved among the ants because of their morphological and behavioral resemblance to the model ant, even when they wandered separately. Presumably, this protects the spider from ant-averse predators. We propose that the spider *M. iguazu* has evolved as a Batesian mimic of the ant *C. sericeiventris*; however, more work must be done to test this hypothesis. Other studies have supported the hypothesis that myrmecomorphic spiders are Batesian mimics (Engelhardt 1970; Cutler 1991; Nelson & Jackson 2006, 2009; Nelson et al. 2006; Huang et al. 2011; Durkee et al. 2011; Nelson 2012). The behavioral experiments provided no support for the hypothesis that the spiders are aggressive mimics because they avoided the models in all tests.

In the field samplings, a lizard (*Tupinambis merinae*) was observed removing a prey (Odonata) that was carried by *C. sericeiventris* workers. The lizard stripped the prey of ants with its front legs without ingesting any of these ants and consumed it. This observation suggests that these ants may be unpalatable to at least some arthropod predators, and that the lizards can recognize ants as undesirable.

Camponotus sericeiventris has a wide distribution in tropical America, and considering its size, its dense reflective pubescence and its populous colonies, it is one of the most conspicuous ants of tropical America. For this reason the model is commonly imitated by different arthropod groups. *Eplophorus velutinus* (Coleoptera: Cerambicidae) in Honduras (Wheeler 1931), *Myrmecotypus rettenmeyeri* in Panama (Reiskind 1965) and *Pappognatha myrmiciformis* (Hymenopera: Mutiliidae) in Panama (Wheeler 1983) have been mentioned as mimetic of *C. sericeiventris*.

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LITERATURE CITED

Cabrera, A.L. & A. Willink. 1973. Biogeografía de América Latina. Monografía 13, Serie de Biología, Washington D.C., USA, Organización de Estados Americanos.

Cuezzo, F. 1998. Formicidae. Pp. 452–462. *In* Biodiversidad de Artrópodos Argentinos, Volume 1. (J.J. Morrone & S. Coscarón, eds.). Ediciones Sur, La Plata, Argentina.

Cushing, P.E. 1997. Myrmecomorphy and myrmecophily in spiders: a review. Florida Entomologist 80:165–193.

Cushing, P.E. 2012. Spider-ant associations: An updated review of myrmecomorphy, myrmecophily, and myrmecophagy in spiders. Psyche 151989:1–23.

Cutler, B. 1991. Reduced predation on the antlike jumping spider *Synageles occidentalis* (Araneae: Salticidae). Journal of Insect Behavior 4:401–407.

Debandi, G. & S. Roig-Juñent. 1999. Especies miméticas de *Camponotus punctulatus* (Formicidae). Revista de la Sociedad Entomológica Argentina 58:201–208.

Durkee, C.A., M.R. Weiss & D.B. Uma. 2011. Ant mimicry lessens predation on a North American jumping spider by larger salticid spider. Environmental Entomology 40:1223–1231.

Engelhardt, W. 1970. Gestalt und Lebensweise der "Ameisenspinne" *Synageles venator* (Lucas) Zugleich ein Beitrag zur Ameisenmimikryforschung. Zoologischer Anzeiger 185:317–334.

Foelix, R. 1996. Biology of spiders, 2nd edition. Oxford University Press, New York.

Galiano, M.E. 1965. Salticidae (Araneae) formiciformes IV. Revisión del genero *Sarinda* Peckham, 1892. Revista del Museo Argentino de Ciencias Naturales 1:267–312.

Galiano, M.E. 1966. Salticidae (Araneae) formiciformes V. Revisión del genero *Synemosyna* Hentz, 1846. Revista del Museo Argentino de Ciencias Naturales 1:339–380.

Galiano, M.E. 1967. Salticidae (Araneae) formiciformes VIII. Nuevas descripciones. Physis 27:27–39.

Galiano, M.E. 1969. Saltieidae (Araneae) formiciformes IX. Adición a las revisiones de los géneros *Martella* y *Sarinda*. Physis 28:247–255.

Galiano, M.E. 1996. Formiciform Salticidae (Araneae). Two new combinations and four new species of the genera *Martella* and *Sarinda*. Miscellania Zoologica 19:107–108.

Hölldobler, B. & E.O. Wilson. 1990. The Ants. Harvard University Press, Cambridge, Massachusetts.

Huang, J.-N., R.-C. Cheng, D. Li & I.-M. Tso. 2011. Salticid predation as one potential driving force of ant mimicry in jumping spiders. Proceedings of the Royal Society B 278:1356–1364.

ITIS (Integrated Taxonomic Information System). 2013, Online at http://www.itis.gov

Joron, M. 2003. Mimicry. Pp. 633–643. *In* Encyclopedia of insects. (R.T. Cardé & V.H. Resh, eds.). Aeademic Press, San Diego, California.

Kempf, W.W. 1972. Catálogo Abreviado das Formigas da Região Neotropical (Hymenoptera: Formicidae). Studia Entomologica 15:1–344.

McIver, J.D. & G. Stonedahl. 1993. Myrmecomorphy: morphologieal and behavioral mimicry of ants. Annual Review of Entomology 38:351–379.

Mello-Leitão, C. 1939. Aracnídios. Boletim Biológico (N. S.) 4:281–294.

Nelson, X.J. 2012. A predator's perspeetive of the accuracy of ant mimicry in spiders. Psyche, Article ID 168549, 5 pp.

Nelson, X.J. & R.R. Jackson. 2006. Vision-based innate aversion to ants and ant mimics. Behavioral Ecology 17:676–681.

Nelson, X.J. & R.R. Jackson. 2009. Collective Batesian mimicry of ant groups by aggregating spiders. Animal Behaviour 78:123–129.

Nelson, X.J., R.R. Jackson, D. Li, A.T. Barrion & G.B. Edwards. 2006. Innate aversion to ants (Hymentoptera: Formicidae) and ant mimics: experimental findings from mantises (Mantodea). Biological Journal of the Linnean Society 88:23–32.

Oliveira, P.S. 1986. Ant-mimicry in some spiders from Brazil. Bulletin de la Société Zoologique de France 111:297–311.

Oliveira, P.S. 1988. Ant-mimicry in some Brazilian salticid and clubionid spiders (Araneae: Salticidae, Clubionidae). Biological Journal of the Linnean Society 33:1–15.

Oliveira, P.S. & I. Sazima. 1984. The adaptive bases of ant-mimicry in a neotropical aphantochilid spider (Araneae: Aphantochilidae). Biological Journal of the Linnean Society 22:145–155.

Oliveira, P.S. & I. Sazima. 1985. Ant-hunting behaviour in spiders with emphasis on *Strophius nigricans* (Thomisidae). Bulletin of the British Arachnological Society 6:309–312.

Pekár, S. & J. Křál. 2002. Mimicry complex in two central European zodariid spiders (Araneae: Zodariidae): how *Zodarion* deceives ants. Biological Journal of the Linnean Society 75:517–532.

Placci, G. & M. Di Bitetti. 2006. Ecorregión Selva Paranaense. Pp. 195–225. *In* La Situación Ambiental Argentina 2005. (A.D. Brown, U. Martínez Ortíz, M. Acerbi & J. Corcuera, eds.). Fundación Vida Silvestre Argentina, Buenos Aires.

Reiskind, J. 1965. The taxonomic problem of sexual dimorphism in spiders and a synonymy in *Myrmecotypus* (Araneae, Clubionidae). Psyche 72:279–281.

Reiskind, J. 1969. The spider subfamily Castianeirinae of North and Central America (Araneae: Clubionidae). Bulletin of the Museum of Comparative Zoology 138:163–325.

Reiskind, J. 1970. Multiple mimetic forms in an ant-mimicking clubionid spider. Science 169:587–588.

Reiskind, J. 1977. Ant-mimicry in Panamanian clubionid and salticid spiders (Araneae: Clubionidae, Salticidae. Biotropica 9:1–8.

Rubio, G.D. & M.O. Arbino. 2009. The first *Myrmecotypus* O. P.-Cambridge (Araneae: Corinnidae) from Argentina: description of *Myrmecotypus iguazu* new species. Zootaxa 2158:65–68.

Simon, E. 1897. Histoire Naturelle des Araignées. Encyclopédie Roret, Paris.

Vane-Wright, R.I. 1976. A unified classification of mimetic resemblance. Biological Journal of the Linnean Society 8:25–56.

Vane-Wright, R.I. 1980. On the definition of mimicry. Biological Journal of the Linnaean Society 70:459–466.

Wheeler, W.M. 1931. The Ant *Camponotus* (*Myrnepomis*) *sericeiventris* Guerin and its mimic. Psyche 38:86–98.

Wheeler, G.C. 1983. A mutillid mimic of an ant (Hymenoptera: Mutillidae and Formicidae). Entomological News 94:143–144.

Wickler, W. 1968. Mimicry in Plants and Animals. Weidenfeld and Nicolson, London.

Yamamoto, M. & K. Del-Claro. 2008. Natural history and foraging behavior of the earpenter ant *Camponotus sericeiventris* Guérin, 1838 (Formicinae, Campotonini) in the Brazilian tropical savanna. Acta Ethologica 11:55–65.

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SHORT COMMUNICATION

Influence of prey availability on seasonal fluctuation in body condition in the wolf spider, *Pardosa milvina* (Araneae: Lycosidae)

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Abstract. Foraging by an organism varies over the season in response to environmental conditions. Predatory arthropods, such as spiders, are frequently in a food-limited state despite their polyphagous habits and may feed opportunistically to enhance rates of growth, survival and reproduction. We predicted that, to circumvent food limitation, spider foraging would be related to prey availability. We examined the extent to which body condition of spiders, a correlate of recent foraging, was related to prey availability and habitat type. Wolf spiders *Pardosa milvina* (Hentz 1844) were collected between May and October in two habitat types, corn and soybean fields. To assess changes in spider condition, we calculated and compared multiple body condition indices derived from morphometric measures of individual spiders. Prey abundance was monitored over the same period using a vacuum suction sampler. Body condition indices provided qualitatively equivalent results. Interestingly, juvenile males were in better condition than adult males, but the opposite was the case for juvenile versus adult females. Although the availability of potential prey generally increased over the growing season, changes in body condition fluctuated independently of prey, suggesting that *Pardosa milvina* have life history differences in foraging and demand for resources that may influence foraging decisions.

Keywords: Foraging, predation, temporal dynamics

Landscape configuration, agricultural management and habitat complexity influence the abundance and diversity of spiders (Clough et al. 2005; Schmidt & Rypstra 2010). The fine-scale effects of management practices on predator biology are complex and often interrelated. For instance, the structure of the environment can influence the foraging rate of predators (Langellotto & Denno 2006) or can provide refuges from risk (Rypstra et al. 2007). Furthermore, the use of pesticides influenees space use and foraging ecology/behavior of spiders (Deng et al. 2008). Although the effects of agricultural practices and landseape patterns on the body condition of spiders has received far less attention (e.g., Öberg 2009; Bucher & Entling 2011), condition indices have proven efficient at predicting important aspects of animal fitness, including recent foraging success (Jakob et al. 1996; Aisenberg et al. 2009), mate choice (Uetz et al. 2002; Pruitt et al. 2011) and sexual cannibalism (Moya-Laraño 2002; Wilder & Rypstra 2008; Pruitt et al. 2011). Body condition indices, calculated using morphometric measurements, show that spiders are commonly food-limited in nature (Bilde & Toft 1998; Wise 2006; Romero & Harwood 2010). Here we explore the seasonal dynamics of body condition of a common agrobiont spider and examine the relationship of body condition to prey abundance in two production systems, corn, *Zea mays* L. (Poales: Poaceae) and soybeans, *Glycine max* L. (Fabales: Fabaceae).

Research was conducted in a previously established experimental agroecosystem located at the Ecology Research Center, Butler County, Ohio, USA (39°31′42″ N, 84°43′48″ W). An array of 12 fields was established, each measuring 60 × 75 m and separated by 15-m grass borders. All fields were managed under standard no-till practices for this region with no insecticides applied at any time during the season. Six of the fields were planted with soybeans (Ebberts seed 1365RR, Ebberts Field Seeds, Covington, Ohio, USA). The other six fields were planted with corn (Steyer Seeds 1095VT3, Steyer Seeds, Tifton, Ohio, USA). None of the fields were sampled twice in the same month, or at the same locations within the field.

The focus of this study was the wolf spider, *Pardosa milvina* (Hentz 1844) (Araneae: Lycosidae). At least 20 spiders were hand collected every two weeks between May and October 2007 in two field types, corn and soybean fields. Hand collecting of spiders occurred by searching the interior of fields and not within 10 m of the edge. Individual spiders were held on ice in 1.5 ml Eppendorf tubes until they could be frozen at −20°C within 2 h. Six fields of each type were sampled throughout the season, and no two fields were sampled on consecutive sampling dates. Frozen spiders were identified to species by inspection of genitalia (Vogel 2004). We know from past studies that *P. milvina* represent 95% of species in the genus *Pardosa* in these fields (Marshall et al. 2002); therefore, although difficult to distinguish, it is unlikely that juveniles were from other species because all adults collected were *P. milvina*. To determine juvenile male or female status, we inspected the genital morphology for sclerotization and associated adult characteristics. In an attempt to control for reproductive status, females with egg sacs were excluded from the analyses. We measured size, cephalothorax width (accuracy ± 0.01 mm), which is a rigid portion of the spider body representative of spider size (Jakob et al. 1996), and mass (accuracy ± 0.1 mg) in the laboratory. Although there are multiple methods to estimate body condition, here we analyzed the data using two common methods [i.e., body mass (García-Berthou 2001) and Scaled Mass Index (Peig & Green 2009)]. We elected to visually display the Scaled Mass Index (SMI) proposed by Peig & Green (2009), which was computed as

$$SMI = M_i\left[\frac{L_o}{L_i}\right]^b$$

where M_i is the body mass, L_i is the cephalothorax width of individual i, b is the scaling parameter estimated by the regression of mass on cephalothorax width and L_o is the arithmetic mean of cephalothorax width value for the study population. Here we focus on the SMI because it is easy to present and interpret, and it scales

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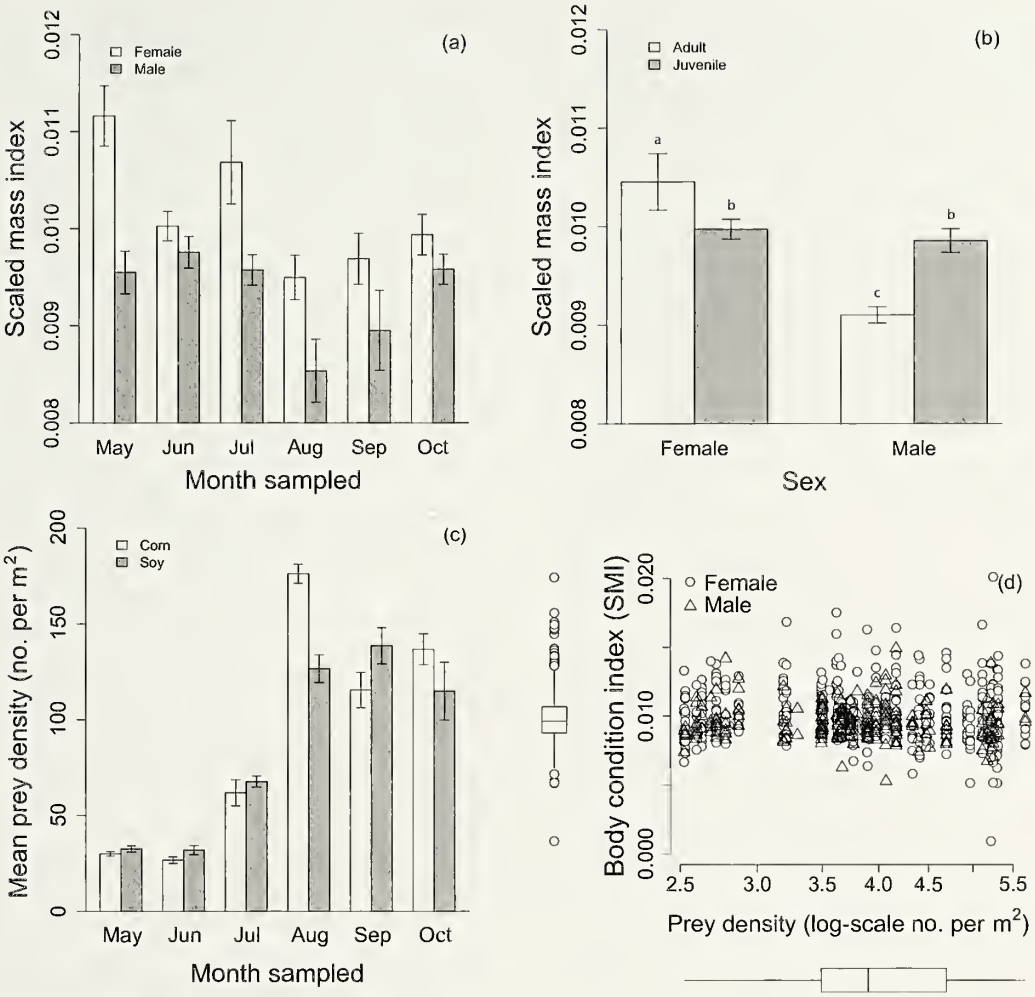

Figure 1.—Body condition (Scaled Body Condition Index, SMI) of *Pardosa milvina* over a growing season in corn and soybean fields in Oxford, Ohio, and the associated density of arthropod prey. Panel (a) represents the mean ± 1 SE fluctuation in body condition during the season for reproductively mature female and males; panel (b) represents the comparison of mean ± 1SE body condition between adult and juvenile males and females (Bonferoni adjusted comparisons are indicated by different letters $P < 0.05$); panel (c) represents the fluctuation in mean ± 1SE arthropod density; and panel (d) represents body condition index (SMI) plotted as a function of prey density (number per m^2) with axis box and whisker bars to represent the distribution of each continuous variable.

body condition according to the size distribution of the spiders sampled. We provide supplemental material on other body condition indices, online at www.bioone.org/doi/suppl/10.1636/P13-18.

Prey abundance was estimated in these same fields by extracting five suction samples ($0.08m^2$/ sample) in both field types on each sample date using a D-VAC suction sampler (Model 24, Rincon-Vitova Insectaries, Ventura, California, USA). Locations for suction sampling were determined by selecting numbers from a random number table to correspond with x, y coordinates of the field such that no locations were sampled within 10 m of the field margin. Suetion samples were sorted to form a prey density estimate (i.e., no. prey/$0.4m^2$). We counted Diptera, Collembola, Homoptera, Thysanoptera, small Orthoptera and small Araneae because these are the groups *Pardosa* are known to consume (Nyffeler 1999). Generalized least squares (GLS, Pinheiro & Bates 2000) analysis models were used to explore the effect of four predictors on body condition: field type, sampling date, spider age and overall prey density.

A total of 732 spiders were collected through the field season (Supplemental Materials, Table S1). Body condition was highly variable over the growing season in both soybean and corn fields (GLS, see Supplemental Materials Table S2; $F_{1,722} = 15.28$, $P = 0.0001$, Fig. 1a), and there were no significant interactive effects of season, field type or prey availability on body condition (GLS, see Supplemental Materials Table S2, 1a).There were significant sex differences in body condition ($F_{1,722} = 7.768$, $P = 0.0055$, Fig. 1b); however, the interaction between age and sex suggests that adult males are typically in poorer condition than juvenile males, and the pattern for females suggests that adults were in better condition than juvenile females ($F_{1,722} = 9.492$, $P = 0.0021$, Fig. 1b). Females were predicted to be in better condition, so this result is not surprising. However, the significant interaction is of interest because this indicates that juvenile males, with unsclerotized pedipalps, were in better condition and may feed more often to increase size. Fitting the different body condition indices, described above, resulted in equivalent qualitative results (Table S2).

Prey density, a variable that should influence the growth and body condition of polyphagous predators, increased over the growing season (GLS, $F_{1,60} = 4.335$, $P < 0.0007$, Fig. 1c; slope estimate on log transformed data = 0.069 (0.02), $t = 3.21$, $P = 0.0014$), and differed between field types sampled ($F_{1,60} = 35.441$, $P < 0.0001$). A significant interaction between field and date sampled indicates that the density of prey in each field type was not consistent over the season ($F_{1,60} = 46.45$, $P < 0.0001$, Fig. 1c). Notably, the densities are similar in May through July, whereas the abundance is higher or

lower between the two field types during August, September and October (Fig. 1c). Although both the condition of predators (Fig. 1a) and availability of prey (Fig. 1c) varied over the season in relation to date and field type, body condition was not significantly related to prey density (see Table S2 for full analysis; $F_{1,722} = 0.59$, $P = 0.442$, Fig. 1d).

Although there was fluctuation in foraging, as indicated by body condition, of male and female *P. milvina* over the growing season within a soybean and corn crop, body condition did not appear to track prey abundance in this system. Inconsistent with other species of spider, body condition is sometimes related to prey availability (Bucher & Entling 2011). Our study suggests that prey availability and field type are not strong predictors of body condition in this wolf spider population. Although our sampling method for prey availability assessed density of prey in a given area, the types that spiders are able to catch or prefer are not necessarily representative of overall abundance. However, based on our results, we emphasize the growing shift in our understanding of the feeding ecology of spiders under field conditions (Chapman et al. 2013). The density of prey alone appears insufficient to predict fitness, especially when prey abundance is high, and for spiders a number of potentially competing prey variables influence foraging decisions. The risk, toxicity (Toft 1999) and nutritional value of prey (reviewed by Wilder 2011) can all affect consumption.

These results indicate life-stage-specific patterns in body condition. Juvenile males must quickly build body tissues by consuming high numbers of prey or selectively consuming high-energy nutrients and protein to fuel fast development (Moya-Laraño et al. 2008). Adult males have reached their growth potential, so low levels of foraging would be sufficient to facilitate mate searching and courtship. In contrast, female foraging responses in short-term laboratory studies indicate that an increase in body condition and number of prey killed is strongly driven by prey density (Walker & Rypstra 2002), but in an open field context we show that body condition was not influenced by prey density. These results suggest that prey selection and foraging strategies during juvenile stages of development do not differ, but the sexes subsequently switch to different strategies following reproductive maturity, where females continue to forage at high levels to improve egg development and males reduce energy needs, only requiring low energy levels to scurry around searching for mates.

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LITERATURE CITED

Aisenberg, A., M. González, Á. Laborda, R. Postiglioni & M. Simó. 2009. Reversed cannibalism, foraging, and surface activities of *Allocosa alticeps* and *Allocosa brasiliensis*: two wolf spiders from coastal sand dunes. Journal of Arachnology 37:135–138.

Bilde, T. & S. Toft. 1998. Quantifying food limitation of arthropod predators in the field. Oecologia 115:54–58.

Bucher, R. & M.H. Entling. 2011. Contrasting effects of habitat fragmentation, population density, and prey availability on body condition of two orb-weaving spiders. Ecological Entomology 36:680–685.

Chapman, E.G., J.M. Schmidt, K.D. Welch & J.D. Harwood. 2013. Molecular evidence for dietary selectivity and pest suppression potential in an epigeal spider community in winter wheat. Biological Control 65:72–86.

Clough, Y., A. Kruess, D. Kleijn & T. Tscharntke. 2005. Spider diversity in cereal fields: Comparing factors at local, landscape and regional scales. Journal of Biogeography 32:2007–2014.

Deng, L., M. Xu, H. Cao & J. Dai. 2008. Ecotoxicological effects of Burprofezin on fecundity, growth, development, and predation of the wolf spider *Pirata piratoides* (Schenkel). Archives of Environmental Contamination and Toxicology 55:652–658.

García-Berthou, E. 2001. On the misuse of residuals in ecology: testing regression residuals vs. the analysis of covariance. Journal of Animal Ecology 70:708–711.

Jakob, E.M., S.D. Marshall & G.W. Uetz. 1996. Estimating fitness: a comparison of body condition indices. Oikos 77:61–67.

Langellotto, G.A. & R.F. Denno. 2006. Refuge from cannibalism in complex-structured habitats: implications for the accumulation of invertebrate predators. Eeological Entomology 31:575–581.

Marshall, S.D., D.M. Pavuk & A.L. Rypstra. 2002. A comparative study of phenology and daily activity patterns in the wolf spiders *Pardosa milvina* and *Hogna helluo* in soybean agroecosystems in southwestern Ohio (Araneae, Lycosidae). Journal of Arachnology 30:503–510.

Moya-Laraño, J. 2002. Senescence and food limitation in a slowly ageing spider. Functional Ecology 16:734–741.

Moya-Laraño, J., R. Macías-Ordóñez, W.U. Blanckenhorn & C. Fernándes-Montraveta. 2008. Analysing body condition: mass, volume or density? Journal of Animal Ecology 77:1099–1108.

Nyffeler, M. 1999. Prey seleetion of spiders in the field. Journal of Arachnology 27:317–324.

Öberg, S. 2009. Influence of landscape structure and farming practice on body condition and fecundity of wolf spiders. Basic and Applied Ecology 10:614–621.

Peig, J. & A.J. Green. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative. Oikos 118:1883–1891.

Pinheiro, J.C. & D.M. Bates. 2000. Mixed-Effects Models in S and S-PLUS. Springer Verlag, New York.

Pruitt, J.N., N. DiRienzo, S. Kralj-Fišer, C. Johnson & A. Sih. 2011. Individual- and condition- dependent effects on habitat choice and choosiness. Behavior Ecology and Sociobiology 65:1987–1995.

Romero, S.A. & J.D. Harwood. 2010. Diel and seasonal patterns of prey available to epigeal predators: evidence for food limitation in a linyphiid spider community. Biological Control 52:84–90.

Rypstra, A.L., J.M. Schmidt, B. D Reif, J. DeVito & M.H. Persons. 2007. Tradeoffs involved in site selection and foraging in a wolf spider: effects of substrate structure and predation risk. Oikos 116:853–863.

Schmidt, J.M. & A.L. Rypstra. 2010. Opportunistic predator prefers habitat complexity that exposes prey while reducing eannibalism and intraguild encounters. Oecologia 164:899–910.

Toft, S. 1999. Prey choice and spider fitness. Journal of Arachnology 27:301–307.

Uetz, G.W., R. Papke & B. Kilinc. 2002. Influence of feeding regime on body size, body condition and a male secondary sexual character in *Schizocosa ocreata* wolf spiders (Araneae, Lycosidae): condition-dependence in a visual signaling trait. Journal of Arachnology 30:461–469.

Vogel, B.R. 2004. A review of the spider genera *Pardosa* and *Acantholycosa* (Araneae, Lycosidae) of the 48 contiguous United States. Journal of Arachnology 32:55–108.

Walker, S.E. & A.L. Rypstra. 2002. Sexual dimorphism in feeding behavior and trophic morphology in wolf spiders (Araneae: Lycosidae). Canadian Journal of Zoology 80:679–688.

Wilder, S.M. & A.L. Rypstra. 2008. Sexual size dimorphism mediates the occurrence of state-dependent sexual cannibalism in a wolf spider. Animal Behaviour 76:447–454.

Wilder, S.M. 2011. Spider nutrition: An integrative perspective. Advances in Insect Physiology 40:87–136.

Wise, D.H. 2006. Cannibalism, food limitation, intraspecific competition, and the regulation of spider populations. Annual Review of Entomology 51:441–465.

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SHORT COMMUNICATION

Comparing ramp and pitfall traps for capturing wandering spiders

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Abstract. Pitfall traps are a common and inexpensive sampling method for epigeal spiders. They are most effective when the top edge of the trap is flush with the soil surface, which is not always possible if soil disturbance is prohibited, the soil layers are thin or the substrate is only exposed rock. Ramp traps are also inexpensive to construct and do not require soil disturbance, making them an appealing alternative to pitfall traps. We tested the efficacy of ramp traps for capturing wandering spiders at the Fort Pierre National Grassland in central South Dakota, USA. We set parallel transects of pitfall and ramp traps during three sampling periods from late May to early August 2010. Ramp traps captured twice as many individuals and, on average, 1.1 ± 0.34 SE more species than pitfall traps. Overall, ramp traps outperformed pitfall traps, and ramp traps are better for non-permanent sampling at point-specific locations.

Keywords: Linyphiidae, Lycosidae, sampling method, temporary trap

Although pitfall traps do not capture all spiders in the community, they are an effective sampling technique for determining the relative abundance and species richness of epigeal spiders (Greenslade 1964; Uetz & Unzicker 1977; Phillips & Cobb 2005). However, to trap effectively, the upper edge of the pitfall should be level with the soil surface, requiring excavation of a small hole into which the pitfall container is inserted. In areas of bare rock (e.g., scree slopes, caves), thin soil horizons over rock, or where soil disturbance is prohibited or requires substantial permitting (e.g., US National Parks), an alternative method of sampling the same epigeal community is desirable.

Bostanian et al. (1983) first described a ramp pitfall trap for capturing large beetles (>10 mm), but their trap structure was heavily biased toward their target taxa. Because the Bostanian et al. (1983) method was expensive and cumbersome to carry into the field, Bouchard et al. (2000) developed a more generalized ramp pitfall trap (hereafter, ramp trap) with greatly reduced cost, weight and size. Pearce et al. (2005) tested these traps and found them effective in reducing vertebrate by-catch. Here we report the results of a short-term study to test the efficacy of ramp traps against pitfall traps for capturing wandering spiders.

The field site was the War Creek Northeast allotment (field) in Stanley County of the Fort Pierre National Grassland (FPNG) in South Dakota, USA. The dominant vegetation is western wheatgrass [*Pascopyrum smithii* (Rydb.) Á. Löve], green needlegrass [*Nassella viridula* (Trin.) Barkworth], buffalo grass [*Buchloe dactyloides* (Nutt.) J.T. Columbus], silverleaf scurfpea [*Pediomelum argophyllum* (Pursh) J. Grimes] and prairie coneflower [*Ratibida columnifera* (Nutt.) Woot. & Standl.]. This field was not grazed at the time of sampling, but it is rotationally grazed (i.e., grazed at different times of the year) by cattle (maybe bison more than five years before this study) and occasionally left to rest without grazing, generally for a period of one to three years. The field is occasionally burned, though not during the decade prior to this study.

In late April 2010, we established five 6-m transects of pitfall traps in the FPNG field. The first transect was chosen near the middle of the field, then the four additional transects were positioned at the main compass points (north, south, east, and west) at least 300 m from the central transect. Each transect consisted of three pitfall traps at 3-m intervals. Each trap consisted of a 10 cm diameter, 20 cm tall PVC sleeve into which a 710 mL plastic cup was inserted and filled to approximately 4 cm depth with 100% propylene glycol. The PVC sleeve was capped on the bottom, and, when not in use, the sleeve was also capped on the top to prevent accidental trapping. To deter trap raiders (e.g., microtine rodents), to prevent captured invertebrates from climbing out of the trap, and to prevent precipitation from directly flooding the trap, an 8-cm powder funnel with its base enlarged to approximately 3 cm was inserted into the cup and a 15 cm × 15 cm board was placed over each trap, leaving approximately 3 cm clearance.

When sampling started, an identical transect of three ramp traps was set 8 m from and parallel to each transect of pitfall traps. Ramp trap design followed Bouchard et al. (2000), with modifications described hereinafter (see Fig. 1). We used 946 mL plastic 12 cm × 12 cm × 8 cm (L × W × H) containers with ramp entrances on

Figure 1.—A typical ramp trap used in this experiment.

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Table 1.—Total numbers of each family (in bold) and species captured in each trap type from Fort Pierre National Grassland, South Dakota, USA. Numbers represent only mature spiders.

Taxon	Pitfalls	Ramps
Agelenidae	**0**	**2**
Agelenopsis emertoni Chamberlin & Ivie 1935	0	2
Clubionidae	**1**	**4**
Clubiona mutata Gertsch 1941	1	4
Corinnidae	**13**	**15**
Castianeira descripta (Hentz 1847)	0	13
Phrurotimpus certus Gertsch 1941	10	2
Scotinella pugnata (Emerton 1890)	3	0
Dictynidae	**2**	**3**
Cicurina arcuata Keyserling 1887	2	0
Dictyna terrestris Emerton 1911	0	3
Gnaphosidae	**54**	**49**
Cesonia bilineata (Hentz 1847)	0	5
Drassodes auriculoides Barrows 1919	1	7
Drassyllus depressus (Emerton 1890)	2	0
Drassyllus nannellus Chamberlin & Gertsch 1940	4	1
Gnaphosa fontinalis Keyserling 1887	14	14
Gnaphosa parvula Banks 1896	1	1
Haplodrassus chamberlini Platnick & Shadab 1975	0	1
Sergiolus decoratus Kaston 1945	0	1
Zelotes hentzi Barrows 1945	31	18
Zelotes laccus (Barrows 1919)	1	1
Linyphiidae	**45**	**44**
Ceraticelus laticeps (Emerton 1894)	6	1
Ceratinops littoralis (Emerton 1913)	0	1
Coloncus siou Chamberlin 1949	0	1
Eridantes erigonoides (Emerton 1882)	10	3
Grammonota vitata Barrows 1919	0	1
Islandiana flaveola (Banks 1892)	12	16
Linyphiidae sp. 1	2	0
Linyphiidae sp. 2	5	0
Linyphiidae sp. 3	1	0
Linyphiidae sp. 4	6	0
Meioneta unimaculata (Banks 1892)	1	1
Mermessus index (Emerton 1914)	0	1
Mermessus sp. 1	2	16
Mermessus trilobatus (Emerton 1882)	0	2
Walkenaeria spiralis (Emerton 1882)	0	1
Lycosidae	**144**	**599**
Hogna frondicola (Emerton 1885)	2	6
Hogna helluo (Walckenaer 1837)	13	5
Pardosa distincta (Blackwall 1846)	42	185
Pardosa modica (Blackwall 1846)	0	2
Piratula minuta (Emerton 1885)	1	0
Schizocosa crassipalpata Roewer 1951	52	317
Schizocosa uccooki (Montgomery 1904)	34	84
Philodromidae	**6**	**90**
Ebo latithorax Keyserling 1884	1	0
Thanatus coloradensis Keyserling 1880	5	84
Thanatus striatus C. L. Koch 1845	0	4
Tibellus chamberlini Gertsch 1933	0	1
Tibellus duttoni (Hentz 1847)	0	1
Salticidae	**11**	**8**
Habronattus viridipes (Hentz 1846)	3	0
Neon nelli Peckham & Peckham 1888	1	0
Phidippus clarus Keyserling 1885	1	1
Phidippus pius Scheffer 1905	1	2
Salticidae sp. 1	0	1
Talavera minuta (Banks 1895)	5	4
Theridiidae	**41**	**41**
Asagena americana Emerton 1882	0	1
Crustulina stricta (O. Pickard-Cambridge 1861)	2	1
Euryopsis saukea Levi 1951	0	2
Theridion petraeum L. Koch 1872	1	1
Theridion pierre Levi & Patrick 2013	38	36
Thomisidae	**148**	**85**
Ozyptila conspurcata Thorell 1887	56	13
Xysticus acquiescens Emerton 1919	2	8
Xysticus bicuspis Keyserling 1887	79	52
Xysticus gulosus Keyserling 1880	4	0
Xysticus luctans (C. L. Koch 1845)	7	12

opposite sides (4 cm cut down from top, 5 cm across). The ramps were cut from sheets of aluminum flashing and the walking surface sprayed with textured spray paint that could be gripped by the spiders. Each ramp trap was filled to approximately 3 cm with 100% propylene glycol. A 38-cm nylon strap with a 20 cm galvanized nail through each end was used to secure the ramp trap in place (nails driven into the substrate), to prevent wind from blowing the trap over and to reduce disturbance by large vertebrates (e.g., browsing deer).

Using the ramp and pitfall traps concurrently, we conducted three sampling periods during 2010: 26 May to 9 June, 23 June to 7 July and 21 July to 5 August. The contents of the pitfall and ramp traps were transferred to Whirl-Pak bags with 100% propylene glycol as the preservative. Mature spiders were later sorted and identified to species (when possible), following Platnick (2013). The numbers of species caught in each trap type during each sampling period were compared using a one-way ANOVA (Minitab Statistical Software version 15.1: Minitab 2007), with number of species caught in each trap as the response variable, and trap type (i.e., pitfall or ramp trap) as the factor.

We captured 1405 mature spiders from 11 families and 60 species (Table 1). Pitfall traps captured 465 mature specimens from 10 families and 41 species, while ramp traps captured 940 specimens from 11 families and 48 species (Table 1). Twelve species were captured only in pitfall traps, and 19 species were captured only in ramp traps. During the first sampling period, pitfall traps captured an average of 5.87 ± 0.38 SE species, while ramp traps captured an average of 7.27 ± 0.44 species (n = 15 for both: Fig. 2). This difference was statistically significant ($F_{1, 28}$ = 5.82, P = 0.023: Fig. 2). During the following two sampling periods, pitfall traps captured an average of 6.00 ± 0.50 and 3.40 ± 0.41 species (Fig. 2), respectively, and ramp traps captured on average 7.27 ± 0.65 and 3.87 ± 0.37 species (Fig. 2), respectively. The difference was not significant for the second ($F_{1, 28}$ = 2.39, P = 0.133) or third ($F_{1, 28}$ = 0.77, P = 0.387) sampling periods. However, pooling all three sampling periods together (n = 45 for each trap type), ramp traps caught significantly more species ($F_{1, 88}$ = 4.79, P = 0.031), with an average of 5.09 ± 0.30 and 6.13 ± 0.37 species, respectively, caught in pitfall traps and ramp traps.

Compared to pitfall traps, ramp traps captured more than twice as many specimens and, on average, one more spider species per trap, making them an effective sampling alternative to pitfall traps. This result is consistent with other studies that have found ramp traps to be effective for capturing other epigeal arthropods (e.g., Goulet et al. 2004; Pearce et al. 2005). Although some species were exclusively caught in only one trap type or the other (Table 1), the common species were captured in both. During the third sampling period, the

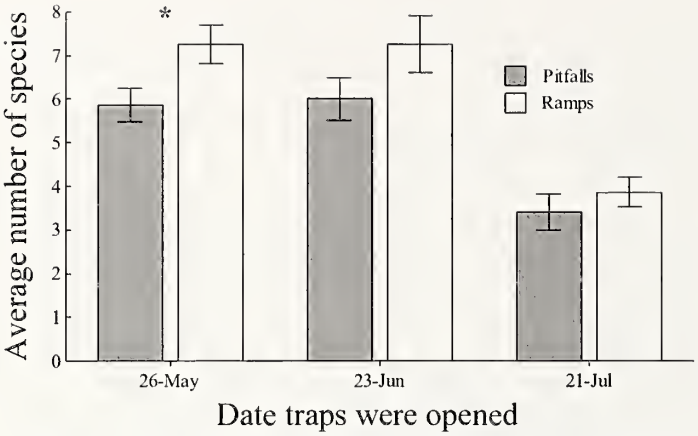

Figure 2.—Mean of species captured in pitfall and ramp traps during each sampling period. (*) indicates a significant difference at $\alpha < 0.05$. Error bars represent ± 1 SE.

convergence of the number of species captured with both sampling methods (Fig. 2) likely occurred because the breeding period for most wandering spiders was largely over, reducing the number of spiders searching for mates. Ramp traps had a higher propensity for singletons and doubletons (Table 1). Although singletons may confound statistical analyses based on abundance, they are valuable for studies seeking to inventory species present in a given area. Thus, the usefulness of ramp traps, like pitfall traps, depends upon the goals of the study.

A pitfall trap is open in all directions, while our ramp traps sampled from two opposite directions. Intuitively, this should reduce the efficacy of ramp traps, since the open space to enter the trap is greatly diminished. However, this clearly was not the case as ramp traps captured more than twice as many spiders. Moreover, ramp traps are fairly versatile and openings may be added to sample in all four directions of a square or rectangular container. Modifications could be made to the ramps to sample virtually in all directions by expanding the width of the base of the ramp, though Bouchard et al. (2000) warn that the ramp design should only be modified slightly for highest efficiency.

Ramp traps are placed on top of the substrate and they are obviously useful in areas where excavation of any kind is impossible, difficult, or prohibited. They are easily set up and emptied, and they require minimal maintenance, though one must be sure that the base of the ramp is as flush as possible with the substrate. However, if substrate excavation is possible and long-term, and repeated sampling in permanent point locations is desired, pitfall traps would be a better sampling method. Using our sampling design (i.e., permanent PVC sleeves left in the field) allows the same locations to be sampled multiple times, which may be desirable for long-term studies.

Ramp traps overcome many of the common problems associated with pitfall traps (Bouchard et al. 2000), such as flooding after heavy rains, dirt falling into the traps, vertebrate by-catch (Pearce et al. 2005) and soil disturbance around the trap. In our study, we did disturb the vegetation slightly to clear a place for the ramp trap, but this resulted in far less disturbance than excavating the substrate. Overall, ramp traps sampled more specimens and more species in the same period of time, making them a viable alternative to traditional pitfall traps.

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LITERATURE CITED

Bostanian, N.J., G. Boivin & H. Goulet. 1983. Ramp pitfall trap. Journal of Economic Entomology 76:1473–1475.

Bouchard, P., T.A. Wheeler & H. Goulet. 2000. Design for a low-cost, covered, ramp pitfall trap. Canadian Entomologist 132:387–389.

Goulet, H., L. Lesage, N.J. Bostanian, C. Vincent & J. Lasnier. 2004. Diversity and seasonal activity of ground beetles (Coleoptera: Carabidae) in two vineyards of southern Quebec, Canada. Annals of the Entomological Society of America 97:1263–1272.

Greenslade, P.J.M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). Journal of Animal Ecology 33:301–310.

Minitab 15 Statistical Software. 2007. Minitab release 15.1.30.0. Minitab Inc., State College, Pennsylvania, USA.

Pearce, J.L., D. Schuurman, K.N. Barber, M. Larrivée, L.A. Venier, J. McKee & D. McKenney. 2005. Pitfall trap designs to maximize invertebrate captures and minimize captures of nontarget vertebrates. Canadian Entomologist 137:233–250.

Phillips, I.D. & T.P. Cobb. 2005. Effect of habitat structure and lid transparency on pitfall catches. Environmental Entomology 34:875–882.

Platnick, N.I. 2013. The world spider catalog, version 13.5. American Museum of Natural History, online at http://research.amnh.org/iz/spiders/catalog

Uetz, G.W. & J.D. Unzicker. 1977. Pitfall trapping in ecological studies of wandering spiders. Journal of Arachnology 3:101–111.

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SHORT COMMUNICATION

Aerial dispersal by *Actinopus* spiderlings (Araneae: Actinopodidae)

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Abstract. Ballooning, a form of dispersal rarely seen in mygalomorph spiders, was observed in 13 individuals of an undetermined species of *Actinopus* under laboratory conditions. After ascending a stick, each spiderling initiated ballooning from either the horizontal lines between sticks or from the stick's edges. They became airborne by dropping and dangling from a dragline, which then gradually lifted and lengthened to 10–15 cm in the breeze, broke at its attachment point, and served as a ballooning thread. This method of ballooning has also been observed in araneomorphs and other species of mygalomorphs, and this is probably a more primitive and shorter distance form of ballooning than that typically practiced by higher araneomorphs, which produce airborne silk lines that are pulled from the spider by air currents and are used either as spanning lines or as balloon lines that allow the spider itself to become airborne.

Keywords: Ballooning, mygalomorph, Argentina

Observations of the dispersal abilities of mygalomorph spiderlings have been rarely reported in the literature and have therefore been an arachnological curiosity, since average mygalomorph spiderlings are far more massive than the corresponding stages of araneomorphs (Coyle et al. 1985). In addition, the observations of ballooning behavior in mygalomorphs could contribute to the understanding of the evolution of aerial webs in other groups and give us insight into the pattern of dispersal from maternal burrows (Eberhard 2005).

Although it is well known that many araneomorph spiders disperse by ballooning (Decae 1987; Suter 1999), ballooning is thought to be only rarely employed by non-araneomorph spiders (Coyle 1983). Previous accounts of ballooning or pre-ballooning behavior in non-araneomorph spiders are easily summarized. The most complete observations are those of Coyle (1983, 1985) and Coyle et al. (1985) of *Sphodros* sp. (Atypidae) and *Ummidia* sp. (Ctenizidae); Eberhard (2005) reported on another *Ummidia* species. Spiderlings of these species moved along bands of silk lines and launched themselves into the air after dangling at the ends of draglines. Enock (1885) observed spiderlings of *Atypus piceus* (Sulzer 1776) (Atypidae) leaving their maternal tubes, trailing draglines and ascending plants, an apparent prelude to ballooning. Baerg (1928) described groups of spiderlings of *Ummidia carabivora* (Atkinson 1886) (Ctenizidae) dispersing from the maternal burrow along wide silk trails to elevated sites, but did not actually observe ballooning. Muma & Muma (1945) also observed silk bands produced by the spiderlings of *Sphodros rufipes* (Latreille 1829), and although they stated that the spiderlings dispersed by ballooning, they did not describe the ballooning process. Cutler & Guarisco (1995) observed a group of spiderlings of *S. fitchi* Gertsch & Platnick 1980 and apparent ballooning attempts at the top of a small tree. Main (1957) suggested that *Conothele malayana* (Doleschall 1859) spiderlings balloon, but only on the basis of observing fine threads of silk produced by spiderlings. Although strongly suggesting that these five mygalomorph species do balloon, these observations are incomplete and have understandably been treated with caution (Bristow 1939; Gertsch & Platnick 1980; Coyle 1983). This note reports an observation of dispersal and ballooning under laboratory conditions by spiderlings of an undetermined species of *Actinopus* (Actinopodidae), the first evidence of ballooning in this family.

One adult female of *Actinopus* sp. was collected on 20 October 2011 at Sierra de la Ventana (38°04′21.3″S, 62°03′02.6″W) (Buenos Aires province, Argentina). Voucher specimens from this study were deposited in the collection of the Laboratorio de Zoología de Invertebrados II, Universidad Nacional del Sur (Bahía Blanca, Argentina). The spider was maintained in a plastic vial (10 cm high and 4.5 cm diameter) with a layer of soil approximately 8 cm deep, allowing the construction and observation of the burrow and trap door. We used a 12 h light/dark cycle, and the room temperature was 26.7 ± 1.52°C. On 28 November 2012, an egg sac was observed inside the burrow. The pale yellow egg sac was nearly hemispherical in shape (diameter 13.3 mm), similar to that reported by Galiano & Goloboff (1996) for *Actinopus* cf. *insignis* (Holmberg 1881). The female's vial was transferred to a glass terrarium 30 × 35 cm and 30 cm high. It was placed on a substrate of polystyrene and two bunches of sticks, 15 cm high, were placed in the center of the container to allow the spiderlings to climb. At about 15:37 on 20 March 2013, an aggregation of four *Actinopus* sp. spiderlings was discovered inside the container. The period of spiderling emergence (during March) was the same as that reported in the field for an *Actinopus* species from the Ventania hilly system in southern Buenos Aires province (Ferretti et al. 2012). The lengths of 46 spiderlings from the dispersal aggregation, including chelicerae and spinnerets, averaged 3.58 mm (range 3.1–4.3 mm). The average width of the prosoma was 1.68 mm (n = 10, range 2.1–3.3). Spiderlings were weighed with an Ohaus PA313 Explorer Precision Balance. Mean spiderling weight was 5.83 mg (n = 12, range = 0.005–0.007).

During 1 h the spiders slowly walked on the silk mats from the burrow entrance and climbed to the margins of the terrarium. Spiderlings migrated in small groups from their mother's burrow to the ballooning site. They emerged one by one from under the lid, which was slightly open, and climbed up along a trail laid by previous spiderlings. At about 18:50 one group of four and one of five spiderlings walked along the silk threads and two of them ascended the sticks by walking and climbed on a dense silk mat 7 mm wide between two sticks (5–6 cm away). Although not observed in detail, previous spiderlings must have made this trip to deposit this dense silk mat. A band of silk about 2 mm wide extended from the margins of the terrarium along the stick surface (8–9 cm). At about 21:00, a fan of 15 cm diameter was placed 50 cm away from the container to generate a consistent air flow of about 200 CFM (cubic feet per minute). The spiderlings moved noticeably faster as they climbed up the ascent routes.

Then, at 21:33, 13 spiderlings ballooned by producing two or more draglines as they walked along horizontal lines. Some kept their spinnerets spread as they walked. Each spiderling walked upside down along aerial cables and ascended the sticks, finally arriving on the tip of the highest sticks. If not yet on the edge of a stick, the spiderling would walk to the edge. It would then tilt its cephalothorax upward, lift its first two pairs of legs and palps off the silk, and extend them out from the stick edge. Then, spiderlings dropped 10 to 15 cm down from the edge on their draglines and dispersed aerially, both from the horizontal lines between sticks and from the stick edges. The spiderlings descended slowly straight downward and facing downward, with their legs spread and immobile. The spinnerets were spread as the spider descended. Eventually the dragline would become long enough that the force of the breeze broke it near its point of attachment to the platform and the dragline, and the attached spiderling drifted through the air.

Successful launchings were observed very infrequently (five cases of 13 observed attempts). More commonly, after dropping on a dragline in the manner just described, the spiderling was either blown against the stick's surfaces (after which it ascended to repeat the launching process) or the spiderling drifted to the ground of the terrarium. By passing our hands through the air between the spiderlings and sticks after launching, we observed that some draglines attached to spiderlings after they were launched.

As observed for other mygalomorph genera, the *Actinopus* spiderlings migrated as a group from their mother's burrow to the ballooning site, forming a strong band of silk (Coyle 1983, 1985; Coyle et al. 1985). Such mass movement, and the resulting formation of compact aerial silk highways, is very unusual in araneomorph spiders. As proposed by Eberhard (2005), spiderlings may benefit from moving as groups; following lines established by nest mates may facilitate rapid movement to ballooning sites. This aerial dispersal mechanism could produce a scattered distribution pattern, as reported for *Sphodros rufipes* and *S. atlanticus* Gertsch & Platnick 1980 (Coyle & Shear 1981). Unfortunately, the spatial distribution of *Actinopus* species in the field has not been studied in detail.

The band of silk observed in this study extending from the margins of the terrarium along the stick surfaces probably marked the ascent route followed by most or all of the brood, as was seen in *Sphodros* sp. (Coyle 1983). As we observed in *Actinopus* spiderlings, both Coyle (1985) and Eberhard (2005) reported that spiderlings of *Unimida* spp. walked with their spinnerets spread, producing at least two lines and probably more. The ability of spiderlings to walk upside down along aerial cables may be a very ancient trait, and as proposed by Eberhard (2005), it could have been important in facilitating the evolution of aerial webs in other groups.

This *Actinopus* method of ballooning by dropping and dangling from a dragline that is lifted and lengthened by the breeze, breaks near the substrate, and finally serves as the ballooning thread, has also been observed in araneomorphs such as dysderids and segestrids (Bristowe 1939, 1958). This is probably a more primitive and shorter distance form of ballooning than that practiced by higher araneomorphs (Coyle 1983), which produce airborne silk lines that are pulled from the spider by air currents and are used either as spanning lines that serve as bridges to distant objects or as balloon lines that allow the spider itself to become airborne (Eberhard 1987). Our observations of *Actinopus* ballooning are compatible with the hypotheses of the initiation of ballooning lines by dragline breaking proposed for other mygalomorphs by Coyle (1983, 1985) and Braendegaard (1938) for dictynid spiderlings.

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Thanks to W. Eberhard and E. Jakob for their valuable comments on the manuscript. Special thanks are due to Pablo Rodriguez, who captured the female of *Actinopus* sp. Also thanks to Leonardo Menescardi, who first noticed the *Actinopus* spiderlings and alerted us. N. Ferretti, G. Pompozzi and S. Copperi are thankful to CONICET for their doctoral and postdoctoral fellowships.

LITERATURE CITED

Baerg, W.J. 1928. Some studies of a trapdoor spider (Araneae: Avicylariidae). Entomological News 39:1–4.

Braendegaard, J. 1938. Aeronautic spiders in the arctic. Medd Gröland 119(5):3–9.

Bristowe, W.S. 1939. The Comity of Spiders. Vol. I. Ray Society, London.

Bristowe, W.S. 1958. The World of Spiders. Collins, London.

Coyle, E.A. 1983. Aerial dispersal by mygalomorph spiderlings (Araneae, Mygalomorphae). Journal of Arachnology 11:283–295.

Coyle, E.A. 1985. Ballooning behavior of *Unimidia* spiderlings (Araneae, Ctenizidae). Journal of Arachnology 13:137–138.

Coyle, E.A. & W.A. Shear. 1981. Observations on the natural history of *Sphodros abboti* and *Sphodros rufipes* (Araneae, Atypidae) with evidence for a contact sex pheromone. Journal of Arachnology 9:317–326.

Coyle, E.A., M.H. Greenstone, A. Hultsch & C.E. Morgan. 1985. Ballooning mygalomorphs: estimates of the masses of *Sphodros* and *Unmidia* ballooners (Araneae: Atypidae, Ctenizidae). Journal of Arachnology 13:291–296.

Cutler, B. & H. Guarisco. 1995. Dispersal aggregation of *Sphodros fitchi* (Araneae, Atypidae). Journal of Arachnology 23:205–206.

Decae, A.E. 1987. Dispersal: ballooning and other mechanisms. Pp. 348–356. *In* Ecophysiology of Spiders (W. Nentwig, ed.). Springer-Verlag, Berlin.

Eberhard, W.G. 1987. How spiders initiate airborne lines. Journal of Arachnology 15:1–9.

Eberhard, W.G. 2005. Dispersal by *Unmidia* spiderlings (Araneae, Ctenizidae): ancient roots of aerial webs and orientation? Journal of Arachnology 34:254–257.

Enock, E. 1885. The life-history of *Atypus piceus*, Sulz. Transactions of the Entomological Society of London 1885:389–420.

Ferretti, N., G. Pompozzi, S. Copperi, F. Pérez-Miles & A. González. 2012. Mygalomorph (Araneae) spider community of a Natural Reserve in a hilly system from central Argentina. Journal of Insect Science 12:31. online at http://insectscience.org/12.31

Gertsch, W. & N. Platnick. 1980. A revision of the American spiders of the family Atypidae (Araneae, Mygalomorphae). American Museum Novitates 2704:1–39.

Galiano, M.A. & P.A. Goloboff. 1996. Postembryonic development of *Actinopus* cf. *insignis* and *Diplura paraguayensis* (Araneae, Mygalomorphae). Bulletin of the British Arachnological Society 10:121–126.

Main, B. 1957. Occurrence of the trap-door spider *Conothele malayana* (Doleschall) in Australia (Mygalomorphae: Ctenizidae). Western Australian Naturalist 5:209–216.

Muma, M.H. & K.E. Muma. 1945. Biological notes on *Atypus bicolor* Lucas. Entomological News 56:122–126.

Suter, R.B. 1999. An aerial lottery: the physics of ballooning in a chaotic atmosphere. Journal of Arachnology 27:281–293.

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SHORT COMMUNICATION

Two new North American *Theridion* species (Araneae: Theridiidae)

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Abstract. Two new species in the genus *Theridion* Walckenaer 1805 (Araneae: Theridiidae) are described: *T. logan*, sp. nov., from Utah, USA, and *T. pierre*, sp. nov., from South Dakota, USA. Diagnoses, descriptions and habitat notes are provided for both sexes of these new species. Both species are from open, grassland-type habitats.

Keywords: cobweb weavers, grassland, prairie, sagebrush steppe

The cosmopolitan genus *Theridion* Walckenaer 1805 has over 570 species worldwide, and over 50 species in North Ameriea north of Mexico (Platnick 2013). The last major taxonomic revisions of North American species of the genus were by Levi (1957, 1963), and there has been recent moleeular phylogenetic work on the genus (Arnedo et al. 2007). Here we report two new North American species in the genus. One of these is from a well-colleeted area near Salt Lake City, Utah, and the other from the Fort Pierre National Grassland in central South Dakota, both collected using pitfall traps. Following Levi (1957, 1963), both speeies are placed in the genus *Theridion* based on the lack of eolulus, the sub-spherieal abdomen, the male palpus with a well-developed radix and median apophysis, and an alveolus of the male palpus that oecupies the whole cymbium.

Specimens were examined using a Leitz dissecting scope, and drawings were made by hand using a reticule with a grid on the dissecting scope eyepiece, and drawn on tracing paper placed on top of gridded paper. Measurements were made using the retieule grid; all measurements are in millimeters. Abbreviations: AMNH - Ameriean Museum of Natural History; MCZ - Museum of Comparative Zoology, Harvard University.

Theridion logan sp. nov.
(Figs. 1–5)

Type material.—Male holotype with 2 female paratypes from Logan Canyon, Caehe Co., Utah, USA. Woodcamp, 41°47.97′N, 111°38.96′W, at 1715 m from sagebrush steppe, 9 July 2008 (coll. S.M. Cobbold) in MCZ.

Etymology.—The species is named after the type locality, the name being a noun in apposition.

Diagnosis.—The species is most similar to *Theridion rabuni* Chamberlin & Ivie 1944 but differs from it as follows: the male median apophysis of *T. logan* has three prongs (MA in Fig. 4), its radix is reduced (R in Fig. 5) and the conductor rises diagonally to the tip (C in Fig. 5); in contrast to *T. rabuni*, the female epigynum of *T. logan* laeks the pair of seeondary depressions within the eentral depression and possesses a posterior transverse sclerotization (PTS in Fig. 3).

Description.—*Female:* Paratype from Logan Canyon. Carapace dusky yellow with blaek marks (Fig. 1). Sternum black. Dorsum of abdomen with median lobed, light band, sides speckled (Fig. 1); venter with a pair of light spots on black (Fig. 2). Anterior median eyes slightly smaller than others, 1.5 diameters apart and less than one diameter from lateral median eyes, others subequal in size. Posterior median eyes one diameter apart from eaeh other and from posterior lateral eyes. Total length 2.2; carapaee 0.7 long, 0.7 wide. First femur 1.0, patella and tibia 1.0, metatarsus 0.7, tarsus 0.5. Second patella and tibia 0.7, third patella and tibia 0.4, fourth patella and tibia 0.7.

Male: Holotype from Logan Canyon. Carapace and sternum slightly lighter than in female. Abdomen as in female. Eye size and spacing as in female. Total length 1.7. Carapace 0.7 long, 0.6 wide. First femur 1.7, patella and tibia 1.2, metatarsus 0.9, tarsus 0.5. Second patella and tibia 0.6, third patella and tibia 0.5, fourth patella and tibia 0.8.

Note.—The thin internal female ducts could not be discerned, the seminal receptacles are pear-shaped, their narrow end to the posterior. The few females available show variation in their epigynum. The seminal receptacles may be closer together and the posterior of the depression wider than in Fig. 3. There is a posterior slit-shaped, transverse depression with a lip (Fig.3), whieh in some is less distinct. The pair of ventral white patehes varies in size.

Other specimens.—*Paratypes:* USA: *Utah*, Cache Co., Hardware Raneh, 41°36.11′N, 111°33.94′W, sagebrush steppe, 25 June 2009, 2 females (coll. L.F. Spears, MCZ); Logan Canyon, Forestry Station, 41°52.42′N, 111°33.74′W, 1915 m, sagebrush steppe, 30 June 2008, 1 male, 2 females (eoll. S. M. Cobbold, AMNH).

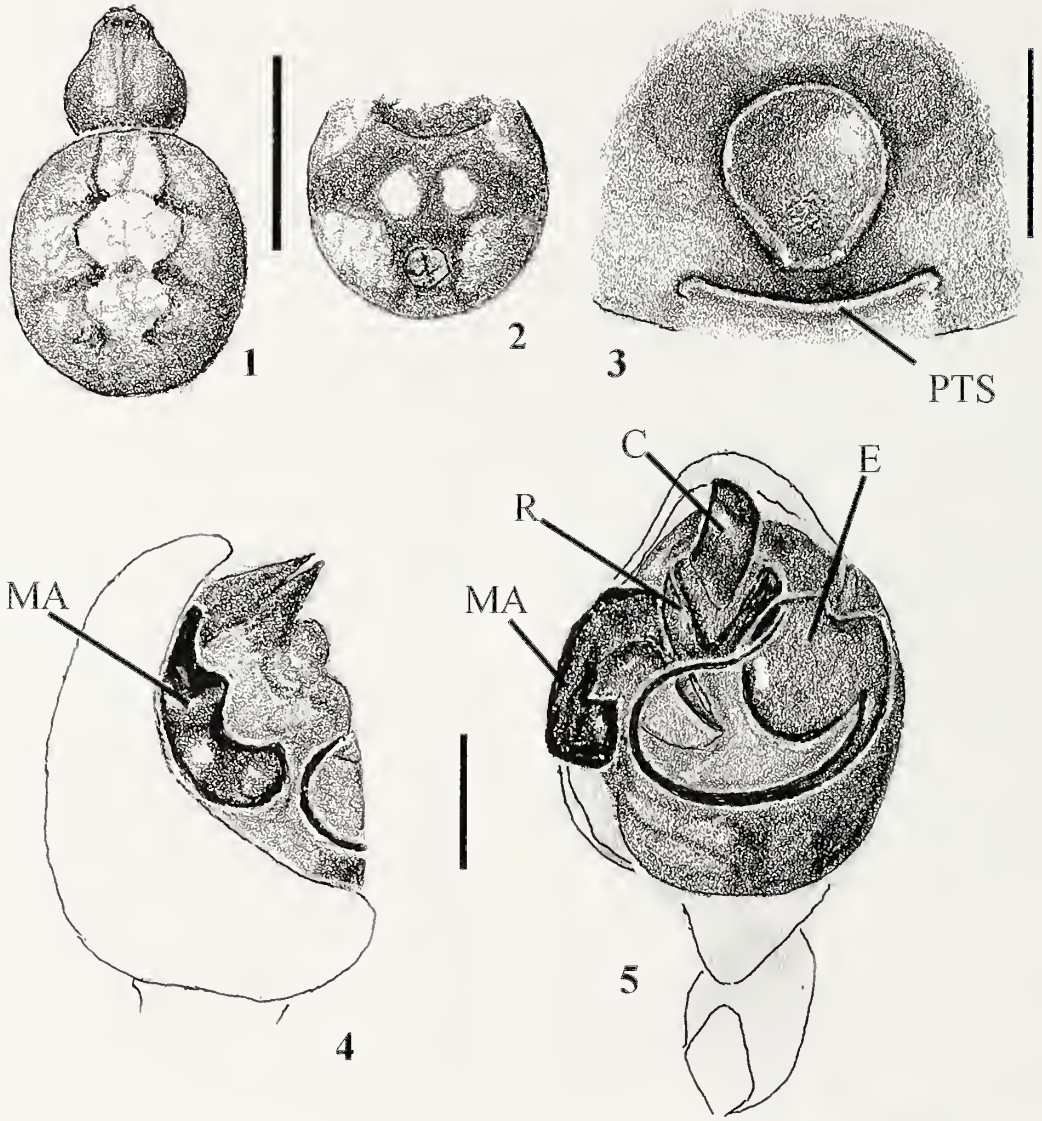
Theridion pierre sp. nov.
(Figs. 6–12)

Type material.—Male holotype, with two male and one female paratypes from Fort Pierre National Grassland, 596 m, Stanley Co., South Dakota, USA, 44°11.52′N, 100°02.52′W, 26 May to 9 June 2010, (eoll. L.B. Patrick, J. Werner, A. Walter) from pitfall traps, in MCZ.

Etymology.—The species is named after the type locality, and the name is a noun in apposition. As the species is named after a location, the proper pronuneiation of the specific epithet should follow the pronunciation of the geographic area of the location. The name of the capital of South Dakota, USA, is Pierre, and is pronounced the same as the American English word "peer."

Diagnosis.—The palpus has a short embolus like *T. dulcineum* Gertseh & Archer 1942 (E in Fig. 12), but differs by having a distal sclerotized hooked eonductor (C in Fig. 12) and by the median apophysis bearing a long tooth (MA in Fig. 11). The epigynum differs from all other *Theridion* species by having an indistinct transverse depression (Fig. 7), whieh may have a copulatory plug (Fig. 8).

Description.—*Female:* Carapaee dusky yellow with black eye region and black line around margin (Fig. 9). Abdomen light gray, with a black mark above and dorsal of spinnerets. Eyes subequal in size. Anterior medians 1.2 apart, 0.3 from laterals. Posterior median eyes one diameter apart from each other, 0.5 diameter apart from posterior lateral eyes. Total length 1.3; carapace 0.6 long, 0.6 wide. First femur 0.7, patella and tibia 0.8, metatarsus 0.6, tarsus 0.4. Second patella and tibia 0.5, third patella and tibia 0.4, fourth patella and tibia 0.6.



Figures 1–5.—*Theridion logan* new species. 1–3, female. 1, habitus, dorsal. 2, abdomen, ventral. 3, epigynum, ventral. 4–5, left male palpus. 4, mesal. 5, ventral. Scale bars = 1.0 mm, and 0.1 mm for genitalia. Abbreviations: C, conductor; E, embolus; MA, median apophysis; PTS, posterior transverse sclerotization; R, radix.

Male: Coloration as in female, with only some black pigment spots between eyes. Eyes subequal. Anterior median eyes one diameter apart from each other, 0.5 diameter from anterior lateral eyes. Posterior median eyes one diameter apart from each other and from posterior lateral eyes. Total length 1.3. Carapace 0.7 long, 0.6 wide. First femur 0.9, patella and tibia 1.0, metatarsus 0.7, tarsus 0.4. Second patella and tibia 0.7, third patella and tibia 0.5, fourth patella and tibia 0.7.

Note.—The thin internal female ducts traverse a loop (Fig. 6). The epigynum (Fig. 7) may have a plug (Fig. 8).

Remarks and Natural History.—All specimens reported here were collected with pitfall traps open for 14 days and containing 100% propylene glycol. The species has been collected from multiple locations within the Fort Pierre National Grassland. The dominant vegetation cover of these northern wheatgrass-needlegrass plains include western wheatgrass (*Pascopyrum smithii*), various needlegrasses (*Stipa* sp.) and blue grama grass (*Bouteloua gracilis*). Additional specimens (not reported here) were caught through litter sifting, with ramp traps and with vacuum sampling. Other spider species commonly caught with this species included *Ozyptila conspurcata* Thorell 1877 (Thomisidae), *Xysticus bicuspis* Keyserling 1877 (Thomisidae), *Schizocosa crassipalpata* Roewer 1951 (Lycosidae), *Pardosa saxatilis* (Hentz 1844) (Lycosidae) and *Eridantes erigonoides* (Emerton 1882) (Linyphiidae).

Other specimens.—*Paratypes*: USA: *South Dakota*, Stanley Co., Fort Pierre National Grassland, pitfall traps, 26 May–9 July 2010, 50 males, 18 females (coll. L.B. Patrick, in MCZ); 2 males,1 female (coll. L.B. Patrick, in AMNH); Sept., Oct. 1 male (coll. L.B. Patrick, in MCZ).

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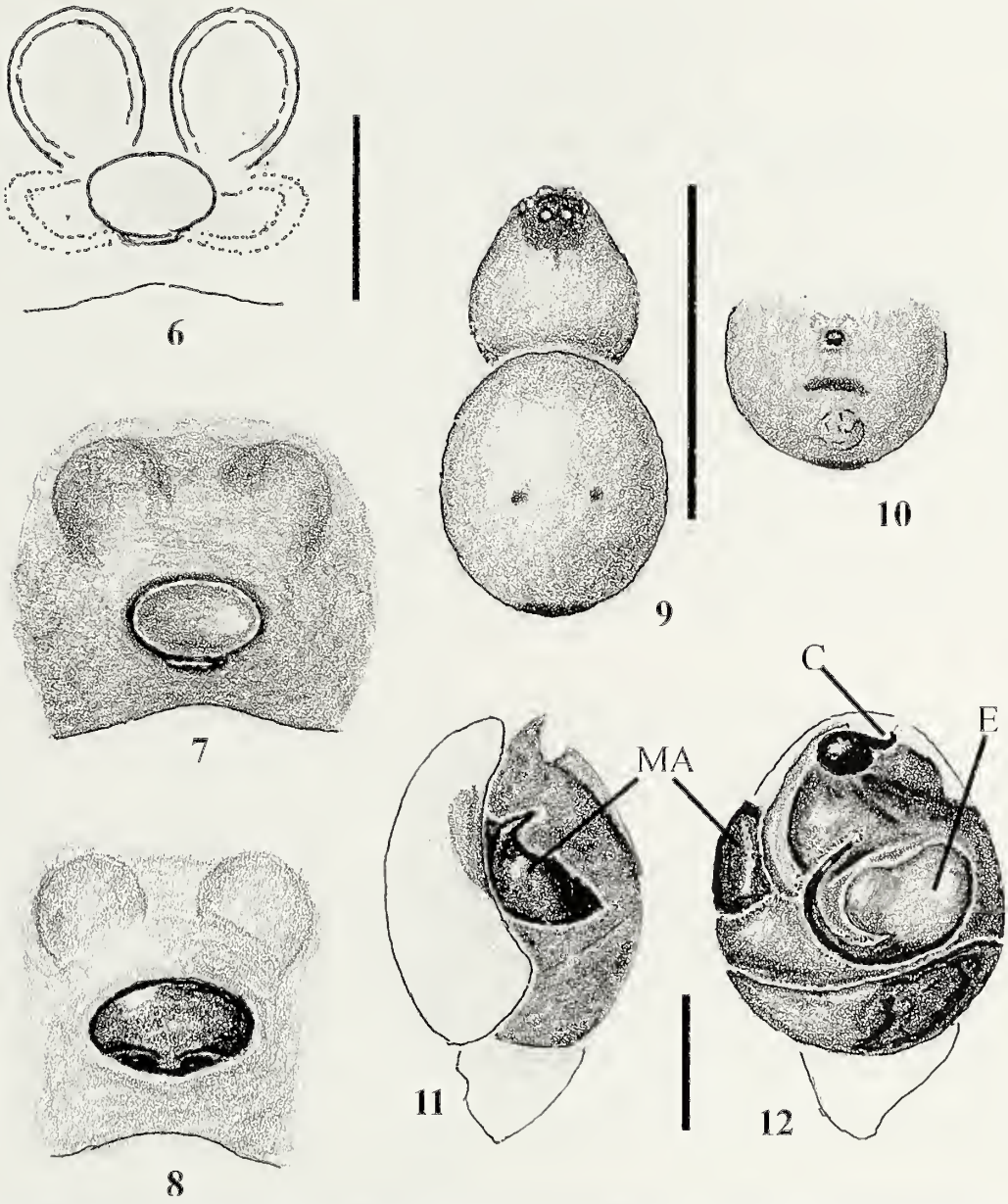

Figures 6–12.—*Theridion pierre* new species. 6–10, female. 6–8, epigynum. 6, cleared. 7, ventral. 8, ventral with plug. 9, habitus, dorsal. 10, abdomen, ventral. 11–12, left male palpus. 11, mesal. 12, ventral. Scale bars =1.0 mm, and 0.1 mm for genitalia. Abbreviations: C, conductor; E, embolus; MA, median apophysis.

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LITERATURE CITED

Arnedo, M.A., I. Agnarsson & R.G. Gillespie. 2007. Molecular insights into the phylogenetic structure of the spider genus *Theridion* (Araneae, Theridiidae) and the origin of the Hawaiian *Theridion*-like fauna. Zoologica Scripta 36:337–352.

Levi, H.W. 1957. The spider genera *Enoplognatha*, *Theridion*, and *Paidisca* in America north of Mexico (Araneae, Theridiidae). Bulletin of the American Museum of Natural History 112:1–123.

Levi, H.W. 1963. American spiders of the genus *Theridion* (Araneae, Theridiidae). Bulletin of the Museum of Comparative Zoology 129:481–589.

Platnick, N.I. 2013. The world spider catalog, version 13.5. American Museum of Natural History, online at http://research.amnh.org/iz/spiders/catalog

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SHORT COMMUNICATION

On the date and organ of publication for the endemic Galápagos scorpion *Centruroides exsul* (Scorpiones: Buthidae) by Wilhelm Meise, with a revision of its distribution and type material

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Abstract. There are conflicting statements in the literature about the date and organ of publication for the endemic Galápagos scorpion *Centruroides exsul* (Scorpiones: Buthidae) by Wilhelm Meise. In contrast to what the current authoritative taxonomic references suggest, this species was not described in 1934 but rather in 1933. Before the article containing the description finally was included in Volume 74 of the Norwegian journal Nyt Magazin for Naturvidenskaberne in 1934, it was distributed as a preprint in the form of Volume 39 of the separately issued series Meddelelser fra det Zoologiske Museum, Oslo in 1933. The latter publication, in full agreement with Article 21.8 of the International Code of Zoological Nomenclature, has priority over the former and consequently has to be referred to when citing the original taxonomic reference. The present contribution furthermore reviews the distribution of this species and, due to loss and mislabeling, revises its type material.

Keywords: Ecuador, nomenclature, South America, taxonomy

Wilhelm Meise (1901–2002) is best known as a gifted and productive ornithologist who, as a doctoral student of Erwin Stresemann (1889–1972) at the Zoological Museum in Berlin in the 1920s and as a contemporary of Ernst Mayr (1904–2005), was part of a prominent group of early twentieth century scientists (Haffer 2003). For detailed information about his personal life and career, see also the accounts by Hoerschelmann (2002, 2003a). While the majority of his publications indeed focus on birds (Hoerschelmann 2003b), Meise showed a wide range of scientific interests and expertise. The most notable of these are probably his work in herpetology, which included the very first two publications of Willi Hennig (1913–1976) (Meise & Hennig 1932, 1935).

During his early years, Meise was employed at the Museum für Tierkunde in Dresden (Germany), where he also undertook an evaluation of the scorpions collected by Alf Wollebæk (1879–1960) during the latter's expedition to the Galápagos Islands in 1925. Wollebæk collected five specimens of a single species of scorpion, which in turn was described by Meise as the new subspecies *Rhopalurus testaceus exsul*.

A review of the Galápagos-relevant scorpion literature, however, revealed conflicting statements about the year and origin of publication for this species, which currently is known as *Centruroides exsul*. Although the name of the author of a given species does not form part of the taxon's name, its citation is strongly advisable (ICZN 1999: Art. 51.1 and Recommendation 51A) and in several journals is fortunately even required. Three different varieties of indication of authorship for this species are known to date:

"*Centruroides exsul* Meise, 1933": Baert (2013): entry no. 93 (p. 15, but not paginated), only by year in the checklist, without citation in the reference section.

"*Centruroides exsul* (Meise, 1933)": Kinzelbach (1973): p. 2.

Maury (1974): p. 19, mentioned only as "*Centruroides exsul* (Meise)" in the text, but with citation of the paper from 1933 in the reference section.

Kinzelbach (1982): p. 118.

Lourenço & Méndez (1984): p. 86 only by year in the text, without citation in the reference section.

Kovařík (2002): p. 6, only by year in the checklist, without citation in the reference section.

"*Centruroides exsul* (Meise, 1934)": Sissom & Lourenço (1987): p. 22.

Fet & Lowe (2000): p. 104.

Since particularly the taxonomic revision by Sissom & Lourenço (1987) and also the comprehensive and authoritative catalog by Fet & Lowe (2000) use the differing "(Meise, 1934)" reference, and at least one of the major on-line taxonomic databases (GBIF 2013) follows this latter allocation, it seems justified to elucidate this formal issue here. This is especially true as not only the year, but also the journal title, differs between Meise (1933) and Meise (1934).

Indeed, there are two independently issued publications, namely the 1933 and the 1934 papers by Meise. However, both have exactly the same content and differ only in the title and heading on the first page (Fig. 1). The publication from 1933 turns out to be an offprint distributed separately and issued in form of the series Meddelelser fra det Zoologiske Museum, Oslo, ahead of the final inclusion of the article in the Nyt Magazin for Naturvidenskaberne in 1934. Although the entire volume of the latter appeared in 1934, Meise's article contains a note at the end that it was previously printed on 14 October 1933 (see Fig. 1). However, according to Article 21.8 of the International Code of Zoological Nomenclature (ICZN 1999), the preprint from 1933 unequivocally has priority and counts as the formal publication containing the species description. Since this paper was distributed as part of an individually and sequentially numbered series (Meddelelser fra det Zoologiske Museum, Oslo), this publication has to be used to give reference to the species description.

Due to certain additional inconsistencies in the literature, especially regarding the type material, it seems appropriate to provide a formal and revised account for this species, which includes the first photographic illustration of the holotype. Institutional abbreviations are NHMO for the Naturhistorisk Museum Oslo (Norway) and SMTD for the Senckenberg Naturhistorische Sammlungen Dresden Museum für Tierkunde (Germany).

Centruroides exsul (Meise 1933)
Fig. 2

Synonymy.—see Kinzelbach (1973:2; 1982:118) and Fet & Lowe (2000:104).

Type specimens.—Holotype female, close to the beach ("Strandregion"), Post Office Bay, Isla Floreana, Galápagos Archipelago, Ecuador, 16–20 September 1925, Alf Wollebæk (NHMO Ga 1062).

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MEDDELELSER FRA DET ZOOLOGISKE MUSEUM, OSLO

Nr. 39

THE NORWEGIAN ZOOLOGICAL EXPEDITION TO THE GALAPAGOS ISLANDS 1925, CONDUCTED BY ALF WOLLEBÆK

VIII.

SCORPIONES

VON

WILHELM MEISE

OSLO 1933

A. W. BRØGGERS BOKTRYKKERI A/S

ⓑ

MEDDELELSER FRA DET ZOOLOGISKE MUSEUM, OSLO. NR. 39

(Særtrykk av Nyt Magazin for Naturvidenskaberne. B 74)

The Norwegian Zoological Expedition to the Galapagos Islands 1925, conducted by Alf Wollebæk

VIII

Scorpiones.

Von

WILHELM MEISE

(Museum für Tierkunde, Dresden)

(Mit 4 Textfig.)

1. Über die Skorpione der Galapagos-Inseln.

Von den Galapagos-Inseln sind bis heute m. W. drei Namen von Skorpionen bekannt geworden. W. Beebe sammelte 1923 auf der Insel Eden (bei Indefatigable) die südamerikanische Art *Hadruroides lunatus* (L. Koch). (W. Beebe, Galapagos, das Ende der Welt, Leipzig 1926, S. 95 u. 346). Der Fischdampfer Albatross hat — wie Marx in Proc. U. S. Nat. Mus. Bd. 12, S. 211, 1889 berichtet — zwei Arten mitgebracht, die durch nomina nuda bezeichnet und m. W. nicht wieder erwähnt worden sind. Die Stelle lautet: »*Centruroides luctifer* sp. nov. From Indefatigable Island, Galapagos; a very interesting species. *Vejovis galapagoensis* sp. nov. From Chatham Island, Galapagos.« Ob die erste dieser beiden Arten mit der unten neu benannten identisch ist, weiß ich nicht.

Über die Herkunft eines Skorpions der Galapagos-Inseln hat N. Banks in Nyt Mag. f. Naturvidenskab. Bd. 68, S. 271, 1931 (= Medd. Zool. Mus. Oslo 22) eine Meinung geäußert, die aber auf einem Irrtum beruht. *Hadruroides lunatus*, den Skorpion aus Südamerika, führt er nämlich als Beispiel für außeramerikanischen Ursprung gewisser Bestandteile der Galapagosfauna an.

Obwohl ich es für möglich halte, daß die Skorpione der Galapagos-Inseln nicht endemisch, sondern vom Menschen eingeschleppt worden sind — und zwar auch die unten benannte Art —, darf ich doch nicht verschweigen, daß schon 1824 von den Leuten Lord Byrons (H. M. S. Blonde) in der Tagusbucht

Nyt Mag. f. Naturv. B LXXIV. 3

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ⓓ Gedruckt 14 Oktober 1933

Figure 1a–d.—Reproductions of the bibliographically relevant aspects from the two publications by Wilhelm Meise. a. Cover sheet of the separately issued and individually bound preprint from 1933; b. Title page of this preprint; c. Title page of the final journal article from 1934, note—in comparison to the preprint from 1933—the lacking extra heading, slightly different vertical arrangement of the title, author's name, etc., but identical body of text; d. Remark on the actual date of printing (14 October 1933) from the end (unpaginated page following p. 43) of the final journal article from 1934.

Paratype: 1 female, same locality as the holotype, 20–30 November 1925, Alf Wollebæk [SMTD "O 691", not available (but see Remarks below)].

Distribution.—Española (= Hood): no specific locality [Banks 1902 (as "*Centrurus princeps* Karsch"); Jackson 1993; Baert 2013]. Floreana (= Santa María, Charles): "Post Office Bay" (type locality); Meise 1933; Kinzelbach 1973; Sissom & Lourenço 1987), no specific locality [Butler 1877 (as "*Androctonus americus* Linnaeus"); Jackson 1993]. Marchena (= Bindloe): "Cabo Espijo Camp" (Sissom & Lourenço 1987). Pinta (= Abingdon): "south coast" (Kinzelbach 1973; Sissom & Lourenço 1987), "south slope" (Sissom & Lourenço 1987), "South Playa" (Sissom & Lourenço 1987), no specific locality (Kinzelbach 1973; Jackson 1993; Kovařík 2002; Baert 2013). San Cristóbal (= Chatham): no specific locality (Kinzelbach 1973; Jackson 1993), "found only at an elevation of 1,000 feet in the interior island" [Snodgrass 1902 (as "*Centrurus princeps*")]. San Salvador (= James, Santiago): no specific locality (Baert 2013). Santa Cruz (= Indefatigable): "Academy Bay" (Kinzelbach 1973; Sissom & Lourenço 1987; Kovařík 2002), "Table Mountain" (Kinzelbach 1973; Sissom & Lourenço 1987), no specific locality [Marx 1890 (as "*Centruroides luctifer* sp. nov.," *nomen nudum*); Kinzelbach 1973; Jackson 1993; Kovařík 2002; Baert 2013].

Figure 2.—The holotype (NHMO Ga 1062) of *Centruroides exsul* (Meise 1933) along with its respective labels. Scale = 5.0 mm. Photo: Karsten Sund, Natural History Museum, University of Oslo, Norway.

Possible non-Galápagos records.—Peru (no specific locality, interpreted as non-native, Sissom & Lourenço 1987), Panamá (Provincia de Chiriquí, record requires confirmation: Lourenço & Méndez 1984).

Remarks.—Beside the one from SMTD (see below), Fet & Lowe (2000:104) list an additional putative female paratype from the Zoologisk Museum Oslo (ZMO, today NHMO, Norway), which most likely has to be regarded as invalid. Meise (1933:27) explicitly designated the specimen with Wollebæk's field number 40 (today, NHMO Ga 1062) as holotype and one specimen (with field number 21) from the Museum für Tierkunde in Dresden (O 691, SMTD, Germany) as paratype. He then wrote that beside these specimens, there were three additional females deposited at NHMO. However, he did not automatically designate them as paratypes, which is evident from the fact that he used the German singular for paratype (= Paratypus) and not the plural (= Paratypen). The whole passage in the original description reads: "Typus im Zoologisk Museum in Oslo, ♀ von Florana (sic), Post Office Bay, Strandregion, Wollebæk leg. Nr. 40 (16.–20. 9. 1925). Paratypus im Museum Dresden O 691, ♀ vom gleichen Fundort, Strandregion, 20.–30. 11.

1925. Wollebæk leg. Nr. 21. Außerdem sind 3 ♀ vom gleichen Fundort im Museum zu Oslo (Nr. 25 ad. u. juv., Nr. 24, September bis Oktober)." Beside the holotype, there are currently four additional specimens deposited at NHMO, to all of which Sissom & Lourenço (1987: p. 22) referred as paratypes. They are still labeled with Wollebæk's field numbers (24: one specimen under Ga 1061; 25: three specimens under Ga 1060). In fact, there seems to be no formal justification to treat any of these as a paratype. The only known initial paratype, originally deposited at SMTD (O 691), is not directly traceable today, although it appears plausible that this is the extra third specimen now deposited under Wollebæk's field number 25 (which, according to Meise, originally were only two). However, due to the lack of an individual label (e.g., the original field tag with number 21) and the lack of any illustrations of the paratype, it is impossible to identify this specimen reliably today.

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I cordially thank Dawn Williams and Karsten Sund (Oslo) for providing information about and photographs of the specimens under their care. Further, I am very grateful to André Reimann (Dresden) for information about the SMTD collection and for valuable discussions. Access to the library of the Naturhistorischer Verein der Rheinlande und Westfalens (Bonn) significantly facilitated this study.

LITERATURE CITED

Baert, L.L. 2013. CDF Checklist of Galapagos Arachnids—FCD Lista des especies de Aracnidos Galápagos (Last updated: 01 Mar 2013). *In* Charles Darwin Foundation Galapagos Species Checklist—Lista de Especies de Galápagos de la Fundación Charles Darwin. (Bungartz, F., H. Herrera, P. Jaramillo, N. Tirado, G. Jiménez-Uzcátegui, D. Ruiz, A. Guézou & F. Ziemmeck, eds.). Charles Darwin Foundation / Fundación Charles Darwin, Puerto Ayora, Online at http://checklists.datazone.darwinfoundation.org/terrestrial-invertebrates/arachnida/

Butler, A.G. 1877. VI. Myriapoda and Arachnida. Pp. 75–77. *In* Account of the Zoological Collection made during the visit of H.M.S. 'Peterel' to the Galapagos Islands.. (A. Günther, ed.). Proceedings of the Zoological Society of London, 45:64–93 + Pls. XI–XIII.

Fet, V. & G. Lowe. 2000. Family Buthidae C. L. Koch, 1837. Pp. 54–286. *In* Catalog of the Scorpions of the World (1758–1998). (V. Fet, W.D. Sissom, G. Lowe & M.E. Braunwalder, eds.). New York Entomological Society, New York.

Global Biodiversity Information Facility [GBIF]. 2013. *Centruroides exsul* (Meise, 1934). Online at http://data.gbif.org/species/6894317

Haffer, J. 2003. Wilhelm Meise (1901–2002), ein führender Ornithologe Deutschlands im 20. Jahrhundert. Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF) 40:117–140.

Hoerschelmann, H. 2002. Wilhelm Meise zum Gedächtnis. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 99:5–9.

Hoerschelmann, H. 2003a. Wilhelm Meise. Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF) 40:141–145.

Hoerschelmann, H. 2003b. Verzeichnis der Schriften von Wilhelm Meise. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 100:153–158.

International Commission on Zoological Nomenclature [ICZN]. 1999. International Code of Zoological Nomenclature. Fourth edition. International Trust for Zoological Nomenclature, London.

Jackson, M.H. 1993. Galápagos—A natural history. Revised and expanded edition, 11th printing 2007. University of Calgary Press, Calgary, Alberta.

Kinzelbach, R. 1973. Scorpions from the Galápagos Islands. Estratto anticipato da: Galápagos Studi e Ricerche Spedizione "L. Mares – G.R.S.T.S.". Gruppo Ricerche Scientifiche e Tecniche Subacquee, Firenze.

Kinzelbach, R. 1982. Scorpions from the Galápagos Islands. Pp. 117–128. *In* Galápagos Studi e Ricerche Spedizione "L. Mares – G.R.S.T.S.". (Anonymous, ed.). Gruppo Ricerche Scientifiche e Tecniche Subacquee, Firenze.

Kovařík, F. 2002. A checklist of scorpions (Arachnida) in the collection of the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany. Serket 8:1–23.

Lourenço, W.R. & E. Méndez. 1984. Inventario preliminar sobre la fauna de escorpiones de Panamá, con algunas consideraciones taxonómicas y biogeográficas. Revista de Biología Tropical 32:85–93.

Marx, G. 1890. Arachnida. Pp. 207–211. *In* Scientific Results of Explorations by the U.S. Fish Commission Steamer Albatross. No. V. Annotated Catalogue of the Insects collected in 1887–88. (L.O. Howard, ed.). Proceedings of the United States National Museum "1889", 12(771):185–216.

Maury, E.A. 1974. Escorpiones y escorpionismo en el Perú. IV: Revisión del genero *Hadruroides* Pocock 1893 (Scorpiones, Vejovidae). Revista Peruana de Entomologia 17:9–21.

Meise, W. 1933. The Norwegian Zoological Expedition to the Galapagos Islands 1925, conducted by Alf Wollebæk. VIII. Scorpiones. Meddelelser fra det Zoologiske Museum, Oslo 39:25–43.

Meise, W. 1934. Scorpiones. Nyt Magazin for Naturvidenskaberne 74:25–43.

Meise, W. & W. Hennig. 1932. Die Schlangengattung *Dendrophis*. Zoologischer Anzeiger 99:273–297.

Meise, W. & W. Hennig. 1935. Zur Kenntnis von *Dendrophis* und *Chrysopelea*. Zoologischer Anzeiger 109:138–150.

Sissom, W.D. & W.R. Lourenço. 1987. The genus *Centruroides* in South America (Scorpiones, Buthidae). Journal of Arachnology 15:11–28.

Snodgrass, R.E. 1902. Field notes on species described in Part I. Pp. 71–80. *In* Papers from the Hopkins Stanford Galapagos Expedition, 1898–1899. VII. Entomological Results (6). Arachnida. (N. Banks, ed.). Proceedings of the Washington Academy of Sciences, 4:49–86.

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SHORT COMMUNICATION

Homolophus bastawadei, a replacement name for the homonym *Euphalangium martensi* (Opiliones: Phalangiidae)

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Abstract. A new name *Honolophus bastawadei* is proposed for *Euphalangium martensi* Das and Bastawade 2006 non Staręga 1986.

Keywords: Nomenclature, new name

The name *Euphalangium martensi* was given by Staręga (1986) for a species from an unspecified locality in eastern Tibet. Twenty years later the same name was used by Das & Bastawade (2006) for another species from the state of Himachal Pradesh in India. Both names are homonyms, and according to the International Code of Zoological Nomenclature (1999) the younger name must be changed. Attempts were made to contact the Indian authors suggesting they make the change by themselves, but with no success.

The situation is even more complicated because the generic name *Euphalangium* Roewer 1911 is not nomenclatorically available any more since Cokendolpher (1987) regarded it as a junior synonym of *Homolophus* Banks 1893. This opinion was confirmed by Tsurusaki et al. (2000), Staręga (2003) and Staręga & Snegovaya (2008).

Taking the above reasons into consideration I feel obliged to propose a new name ***Homolophus bastawadei*** nom. nov. to replace *Euphalangium martensi* Das & Bastawade 2006. It is given in honor of the well-known Indian arachnologist, Dr. Deshbhushan B. Bastawade.

LITERATURE CITED

Cokendolpher, J.C. 1987. On the identity of the genus *Homolophus*: a senior synonym of *Euphalangium* (Opiliones: Phalangiidae). Acta Arachnologica 35:89–96.

Das, N.P.I. & D.B. Bastawade. 2006. A new species of genus *Euphalangium* Roewer (Opiliones: Phalangidae) from western Himalayan region of India. Zoos' Print Journal 21:2207–2209.

International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature, fourth edition. International Trust for Zoological Nomenclature: London.

Staręga, W. 1986. Zwei neue Weberknecht-Arten aus Tibet (Arachnida: Opiliones: Phalangiidae). Senckenbergiana Biologica 67: 131–136.

Staręga, W. 2003. On the identity and synonymies of some Asiatic Opilioninae (Opiliones: Phalangiidae). Acta Arachnologica 52:91–102.

Staręga, W. & N. Yu. Snegovaya. 2008. New species of Opilioninae (Opiliones: Phalangiidae) from the mountains of Kyrgyzstan, Tadjikistan and Uzbekistan. Acta Arachnologica 57:75–85.

Tsurusaki, N., A.N. Tchemeris & D.V. Logunov. 2000. Two new species of Opiliones from southern Siberia and Mongolia, with an establishment of a new genus and redefinition of the genus *Homolophus* (Arachnida: Opiliones: Phalangiidae). Acta Arachnologica 49:73–86.

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SHORT COMMUNICATION

On *Speleosiro argasiformis*—a troglobitic Cyphophthalmi (Arachnida: Opiliones: Pettalidae) from Table Mountain, South Africa

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Abstract. We report the recent collection and observation of large numbers of specimens of the troglobitic harvestman *Speleosiro argasiformis* Lawrence 1931 in the Wynberg Cave system, Table Mountain, South Africa. Specimens were collected and/or photographed in different caves of the system. Live observation showed specimens fleeing bat carcasses when disturbed.

Keywords: Wynberg cave, Gondwana

Cyphophthalmi or mite-harvestmen are mostly known from pristine forests in continental landmasses and islands of continental origin, and some species are known to inhabit cavernicolous environments. Cave cyphophthalmids are not uncommon, with several species described from around the globe (e.g., Juberthie 1971; Rambla and Juberthie 1994; Schwendinger et al. 2004). But only a few of these are true troglobites (also called troglomorphs or troglobiomorphs), possessing morphological adaptations such as lighter pigmentation, reduced eyes, and elongated appendages. Of these true troglobites, most species have small distribution areas and often are the only representatives within their respective families that show such adaptations. This results in a long list of described monotypic genera of cyphophthalmid troglobites, including *Tranteeva* Kratochvíl 1958 (Sironidae; now in *Cyphophthalmus* Joseph 1868), *Shearogovea* Giribet 2011, and *Marwe* Shear 1985 (of uncertain affinities), *Canga* DaSilva, Pinto-da-Rocha & Giribet 2010 (Neogoveidae, although this species is probably a troglophile or even a trogloxene), a few stylocellids (e.g., *Fangensis* Rambla 1994), and *Speleosiro* Lawrence 1931 (Pettalidae), the latter being the subject of this note.

The first true troglobiomorphic cyphophthalmid described with elongated appendages and large body size was *Speleosiro argasiformis* Lawrence 1931 from Wynberg Cave in Table Mountain (Western Cape Province, South Africa) (Lawrence 1931). *Speleosiro argasiformis* is the only member of the Gondwanan family Pettalidae that inhabits the dark zone of caves, despite the high diversity of pettalids in New Zealand (Forster 1948, 1952; Boyer and Giribet 2009), Australia (Juberthie 1989; Giribet 2003; Boyer and Reuter 2012), Chile (Shear 1993), and South Africa (Hansen and Sørensen 1904; Lawrence 1931, 1933, 1939, 1963; de Bivort and Giribet 2010). Here we summarize the knowledge on *S. argasiformis*, accompanied with new data and observations on its abundance and behavior in different caves of the Wynberg cave system.

We have studied all known specimens of *S. argasiformis*, including those deposited in museum collections. We also review all the literature citations known to us. In addition, we provide new observations on collections made by the authors during a visit to the Wynberg cave system on 5 November 2011. Additional photographic material was available from prior visits to the caves by A. Hitchcock and P. Swart. Newly acquired specimens are deposited in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (USA; MCZ IZ-134759-134762). Historical specimens are deposited in the South African Museum, Cape Town, Western Cape Province (South Africa; SAM), or in the Natal Museum, Pietermaritzburg, KwaZulu-Natal (South Africa, NMSA).

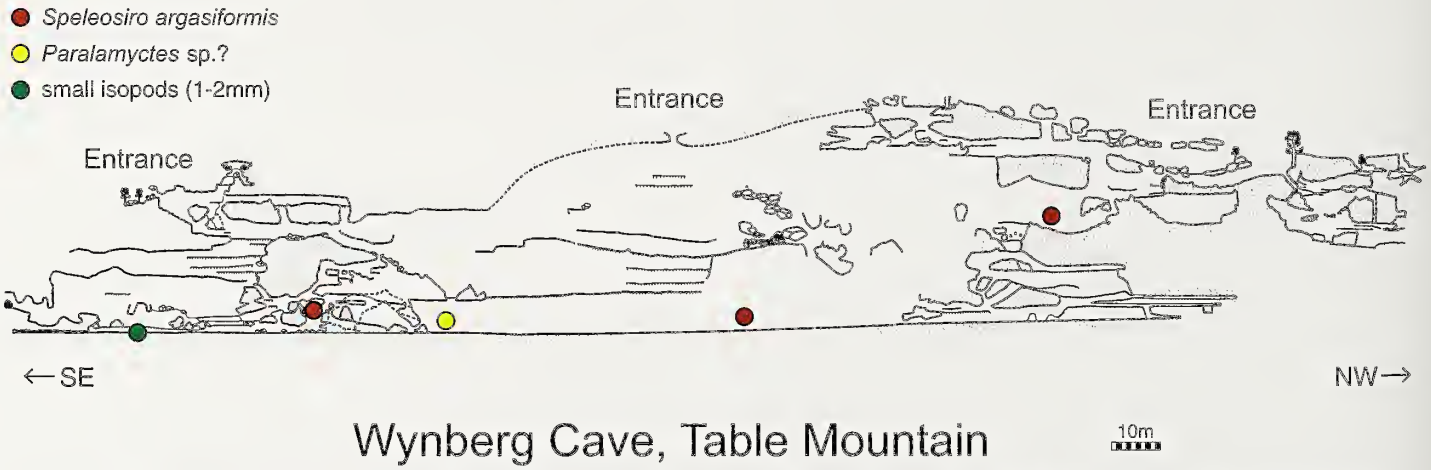

Figure 1.—Profile of the Wynberg Cave system, with localities where *S. argasiformis* was located. Other new arthropod species are indicated.

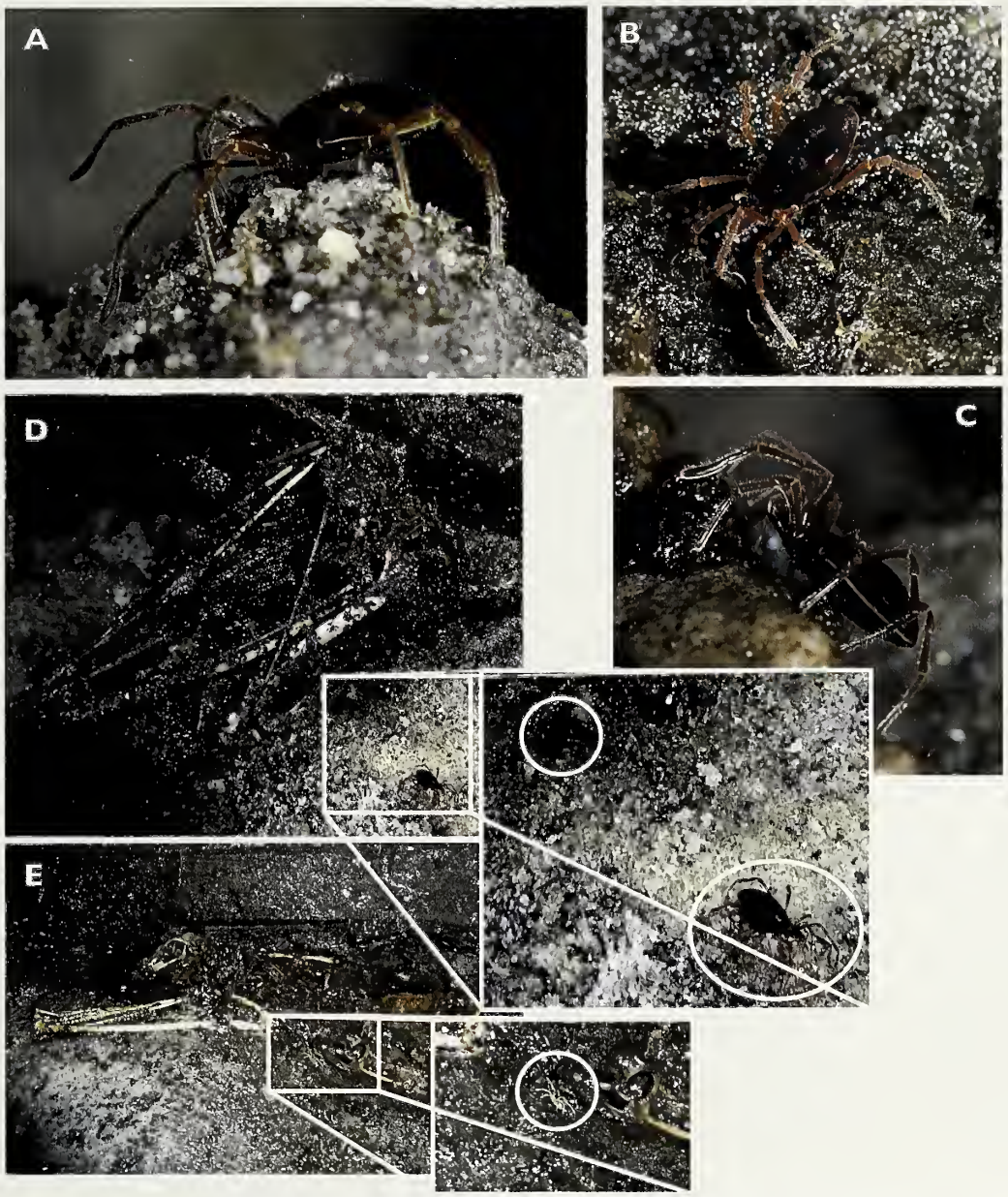

Figure 2.—A. Male adult individual near entrance (right red dot in Fig. 1). B. Adult female near cave entrance. C. Adult female near cave entrance. D. Bat carcass with a fleeing *Speleosiro* specimen and the rear end of another specimen under the carcass visible (see inset). E. A different bat carcass in the bottom of the cave (mid red dot in Fig. 1) with a juvenile specimen fleeing after being disturbed.

Material examined.—*Type material:* SOUTH AFRICA: *Western Cape Province*: holotype female, Wynberg Caves, 1913, K.H. Barnard (SAM B1473).

Other material examined: SOUTH AFRICA: *Western Cape Province*: 1 male, 2 juv., Wynberg Caves (NMSA 7660) (the two subadult females reported as additional material in the original description; the male described on p. 503) (see below); 1 male, 1 female, Bat's Cave, November 1960, N. Leleup (NMSA); 1 female, Wynberg Caves, 30 July 1988, M. Bing (NMSA 14657); 1 female, Bat's Cave, 1956, University of Cape Town Ecological Survey (SAM C2022); 1 female, Wynberg Caves, under rocks, 25 September1960 (SAM C2023); 8 specimens, Wynberg Cave, 5 November 2011 (MCZ IZ-134759); 1 male, Wynberg Cave, 5 November 2011 (MCZ IZ-134760); 1 female, Wynberg Cave, 5 November 2011 (MCZ IZ-134761); 2 females, 1 juv., Inukshuk Cave, 5 November 2011 (MCZ IZ-134762). (We differentiate between Wynberg Caves in the old labels, and Wynberg Cave in the new collections, as the caves system has been mapped recently but the older labels referred to as the entire Wynberg Cave system and it is unclear whether "Wynberg Caves" refers to what it is currently recognized as Wynberg Cave or to any of the other connected caves.)

Geographic and geologic setting.—All specimens have been collected from three caves in the Wynberg Cave system (referred to as "Wynberg Caves" in the older collections): Wynberg Cave, Bat's Cave, and Inukshuk Cave. A physical mapping of the system was undertaken by the South African Spelaeological Association (Cape Town), with participation from A. Hitchcock and P. Swart. A detailed profile of the system and the location of specimens are provided in Figure 1.

Specimens of *Speleosiro argasiformis* (Fig. 2) have been observed in three caves: Wynberg, Inukshuk, and Bat's Cave. This species is especially abundant in Wynberg Cave, where ca. 25 specimens were

seen in different galleries in all the main levels of the cave (Fig. 1). The largest concentration of individuals occurred in the dark zone near the entrance, at a site where small stones and bat guano accumulated (right red dot in Fig. 1). The second largest aggregation occurred on a decaying bat's carcass, covered in guano (Fig. 2D), where we saw three specimens fleeing the carcass after being exposed to light. Another specimen was also observed under a second bat carcass (Fig. 2E). We also noticed several individuals walking about the cave's floor or lower part of the walls, or under medium-sized stones (stones larger than 5 cm in diameter), always in the dark, humid zone of the cave. Associated troglobitic fauna included other Opiliones (*Speleomontia cavernicola* Lawrence 1931), and the rare Neopilionidae *Vibone vetusta* Kauri 1961, several species of spiders, pseudoscorpions, isopods (Crustacea: Malacostraca: Isopoda), an undescribed centipede in the genus *Paralamyctes* (Chilopoda: Lithobiomorpha: Henicopidae), and the troglophile camel cricket *Speleiacris tabulae* (Orthoptera: Rhaphidophoridae). Perhaps the most spectacular is the blind albino velvet worm *Peripatopsis alba* Lawrence 1931. Most of these species are considered to be endangered or critically endangered, as is the case with *P. alba* (Hamer et al. 1997; Sharratt et al. 2000).

Speleosiro argasiformis is poorly known from museum collections and has been considered a "rare species." Referring to the type specimens of this species, Lawrence (1931:350–351) states:

> "These 3 specimens were found in the Wynberg Cave of Table Mountain, one by Dr. K. H. Barnard in 1913 [specimen SAM B 1473], the other two by myself in May 1929. [These are the two subadult females from lot NMSA 7660; the male was later described in p. 503.] The cave occurs at the top of the mountain in the Table Mountain sandstone; the entrance to the caves is tortuous and narrow, and the main body of it where the specimens were found is about 100 feet below the surface, the possibility of any light reaching it being thus precluded; the walls of the main cave are damp and slimy from the water which constantly percolates through fissures in the rocks; the specimens were found under small stones on very damp or even wet sand. The only vegetation seems to consist of a small lichen and the fauna is sparse, the chief representative being the peculiar Acridiid Orthopteron *Speleiacris tabulae*; another peculiar animal inhabiting the cave is a blind and unpigmented Peripatus, *Peripatopsis alba*. Outside at the mouth of the cave were found specimens of *Purcellia illustrans* in the usual habitat."

Juberthie (1970, 1971) provided further details and an accurate redescription of *S. argasiformis*, expanded by de Bivort & Giribet (2010), but no new material was reported by any of these authors. Sharratt et al. (2000) studied the cave fauna of the Cape Peninsula and reported 14 specimens of *S. argasiformis* (misspelled as *S. argasiformes*). These authors proposed that *S. argasiformis*, along with most of the other endemic carvernicoles, be considered Endangered under IUCN Red List Categories, due to their limited distributions. The estimated abundances for Wynberg and Bats' Caves were 0.494 ± 0.63 individuals/m^2 (0.282 for Wynberg and 0.707 for Bats' Cave).

One of the arguments provided by Sharratt et al. (2000) for the conservation status of *S. argasiformis* is its phylogenetic uniqueness, for being the only member of its genus. Morphological cladistic analyses suggest that *Speleosiro* is related to *Purcellia* (de Bivort et al. 2010; de Bivort and Giribet 2010; Giribet et al. 2012), but do not resolve its exact position with respect to the *Purcellia* species. In fact, Lawrence suggested that *Speleosiro argasiformis* is a troglobitic version of the surface species *Purcellia illustrans*. Preliminary molecular data (results not shown) corroborate the monophyly of *Purcellia* + *Speleosiro* (three species of *Purcellia* and *Speleosiro* are identical for 18S rRNA); however, *Speleosiro* is closer to *P. leleupi* and *P. griswoldi* than to the sympatric species *P. illustrans*, according to cytochrome *c* oxidase subunit I data.

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LITERATURE CITED

Boyer, S.L. & G. Giribet. 2009. Welcome back New Zealand: Regional biogeography and Gondwanan origin of three endemic genera of mite harvestmen (Arachnida, Opiliones, Cyphophthalmi). Journal of Biogeography 36:1084–1099.

Boyer, S.L. & C.N. Reuter. 2012. New species of mite harvestmen from the Wet Tropics of Queensland, Australia, with commentary on biogeography of the genus *Austropurcellia* (Opiliones: Cyphophthalmi: Pettalidae). Journal of Arachnology 40:96–112.

de Bivort, B., R.M. Clouse & G. Giribet. 2010. A morphometrics-based phylogeny of the temperate Gondwanan mite harvestmen (Opiliones, Cyphophthalmi, Pettalidae). Journal of Zoological Systematics and Evolutionary Research 48:294–309.

de Bivort, B. & G. Giribet. 2010. A systematic revision of the South African Pettalidae (Arachnida: Opiliones: Cyphophthalmi) based on a combined analysis of discrete and continuous morphological characters with the description of seven new species. Invertebrate Systematics 24:371–406.

Forster, R.R. 1948. The sub-order Cyphophthalmi Simon in New Zealand. Dominion Museum Records in Entomology 1:79–119.

Forster, R.R. 1952. Supplement to the sub-order Cyphophthalmi. Dominion Museum Records in Entomology 1:179–211.

Giribet, G. 2003. *Karripurcellia*, a new pettalid genus (Arachnida: Opiliones: Cyphophthalmi) from Western Australia, with a cladistic analysis of the family Pettalidae. Invertebrate Systematics 17:387–406.

Giribet, G., P.P. Sharma, L.R. Benavides, S.L. Boyer, R.M. Clouse, B.L. de Bivort, D. Dimitrov, G.Y. Kawauchi, J. Murienne & P.J. Schwendinger. 2012. Evolutionary and biogeographical history of an ancient and global group of arachnids (Arachnida: Opiliones: Cyphophthalmi) with a new taxonomic arrangement. Biological Journal of the Linnean Society 105:92–130.

Hamer, M.L., M.J. Samways & H. Ruhberg. 1997. A review of the Onychophora of South Africa, with discussion of their conservation. Annals of the Natal Museum 38:283–312.

Hansen, H.J. & W. Sørensen. 1904. On two orders of Arachnida: Opiliones, especially the suborder Cyphophthalmi, and Ricinulei, namely the family Cryptostemmatoidae. Cambridge University Press, Cambridge, UK.

Juberthie, C. 1970. Les genres d'opilions Sironinae (Cyphophthalmes). Bulletin du Muséum National d'Histoire Naturelle, 2e série 41: 1371–1390.

Juberthie, C. 1971. Les opilions cyphophthalmes cavernicoles. Notes sur *Speleosiro argasiformis* Lawrence. Bulletin du Muséum National d'Histoire Naturelle 42:864–871.

Juberthie, C. 1989. *Rakaia daviesae* sp. nov. (Opiliones, Cyphophthalmi, Pettalidae) from Australia. Memoirs of the Queensland Museum 27:499–507.

Juberthie, C. 1991. Sur *Trenteeva paradoxa* (Kratochvil, 1958), opilion troglobie et les opilions cyphophthalmes de Bulgarie. Mémoires de Biospéologie 18:263–267.

Lawrence, R.F. 1931. The harvest-spiders (Opiliones) of South Africa. Annals of the South African Museum 29:341–508.

Lawrence, R.F. 1933. The harvest-spiders (Opiliones) of Natal. Annals of the Natal Museum 7:211–241.

Lawrence, R.F. 1939. A contribution to the opilionid fauna of Natal and Zululand. Annals of the Natal Museum 9:225–243.

Lawrence, R.F. 1963. The Opiliones of the Transvaal. Annals of the Transvaal Museum 24:275–304.

Rambla, M. & C. Juberthie. 1994. Opiliones. Pp. 215–230. *In* Encyclopaedia Biospeologica. (C. Juberthie and V. Decu, eds.). Société de Biospéologie, Moulis-Boucarest.

Schwendinger, P.J., G. Giribet & H. Steiner. 2004. A remarkable new cave-dwelling *Stylocellus* (Opiliones, Cyphophthalmi) from Peninsular Malaysia, with a discussion on taxonomic characters in the family Stylocellidae. Journal of Natural History 38:1421–1435.

Sharratt, N.J., M.D. Picker & M.J. Samways. 2000. The invertebrate fauna of the sandstone caves of the Cape Peninsula (South Africa): patterns of endemism and conservation priorities. Biodiversity and Conservation 9:107–143.

Shear, W.A. 1993. The genus *Chileogovea* (Opiliones, Cyphophthalmi, Petallidae [sic]). Journal of Arachnology 21:73–78.

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SHORT COMMUNICATION

A new species of *Protoschizomus* (Schizomida: Protoschizomidae) from a cave in Guerrero, Mexico

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Abstract. A new species of the genus *Protoschizomus* Rowland 1975 is described with adult males and females. We collected *Protoschizomus franckei* new species from Cueva del Diablo in the state of Guerrero, Mexico. Currently, the genus *Protoschizomus* is composed of eight species including the new species described here, of which five have been found inside caves.

Keywords: Endemism, schizomids, taxonomy, troglobite

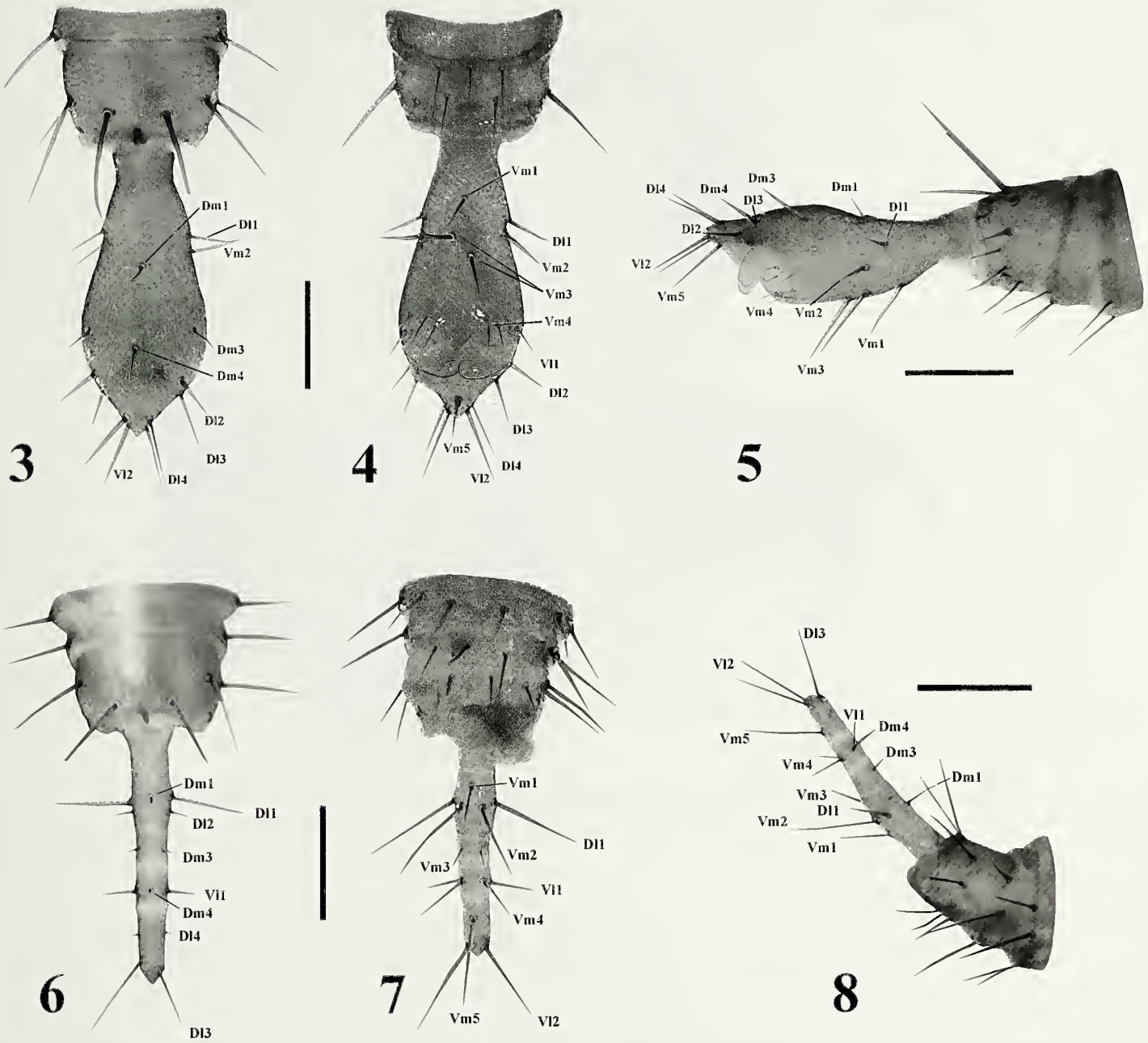
The family Protoschizomidae is a small group of schizomids currently composed of two genera: *Agastoschizomus* Rowland 1971 with five species, all troglobitic, and *Protoschizomus* Rowland 1975 with seven species of which four are also troglobitic (Cokendolpher & Reddell 1992; Harvey 2003; Montaño-Moreno & Francke 2009). The members of this family are considered troglobites because they have undergone several morphological adaptations for living in caves, such as elongated appendages, lack of pigment, lack of ocelli and relatively large body. Actually, *Agastoschizomus lucifer* Rowland 1971, with a body of 12 mm length, is the largest schizomid in the world (Rowland 1971; Cokendolpher & Reddell 1992).

The family is endemic to Mexico and is distributed throughout the states of Colima, Guerrero, Hidalgo, San Luis Potosí, and Tamaulipas (Cokendolpher & Reddell 1992; Montaño-Moreno & Francke 2009). These states have extensive karst formations where limestone is abundant and therefore also have numerous caves. Currently, there are approximately 7,000 caves reported for Mexico (Lazcano 1983), so there are still many caves in which new schizomids might be found.

Recent contributions regarding this family were made by Reddell & Cokendolpher (1992) and Montaño-Moreno & Francke (2009). Reddell & Cokendolpher (1992) revised and described seven new species and proposed two species-groups in *Protoschizomus* based on the shape of the male flagellum, the number of setae on the propeltidium, and the distribution of setae on the sternites, and introduced the nomenclature for the setation of the female flagellum. Montaño-Moreno & Francke (2009) described *Agastoschizomus juxtlahuacensis* Montaño-Moreno & Francke 2009, collected from a cave in the state of Guerrero and representing the second species from western Mexico.

Four of the seven known species of *Protoschizomus* have been collected inside caves (Cokendolpher & Reddell 1992), about 500 to 700 m from the entrance. The caves where these species have been collected are extensive systems, receiving massive amounts of

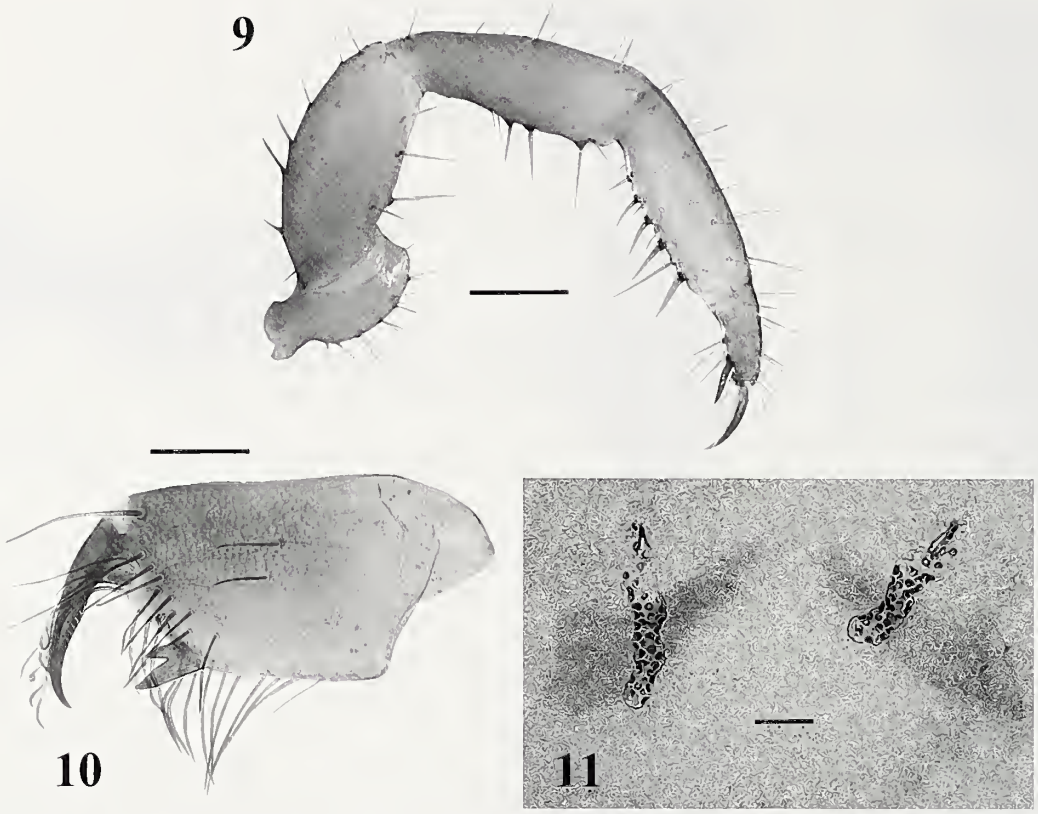
Figures 1–2.—*Protoschizomus franckei* new species. Male holotype. Habitus: 1. Dorsal view. 2. Lateral view. Scale bars = 2 mm.



Figures 3–8.—*Protoschizomus franckei* new species: 3–5. Male holotype, flagellum: 3. Dorsal view; 4.Ventral view; 5. Lateral view. 6–8. Female paratype, flagellum: 6. Dorsal view; 7. Ventral view; 8. Lateral view. Scale bars = 0.2 mm. Setal terminology after Reddell & Cokendolpher (1992): Dm: dorsal median setae; Dl: dorsal lateral setae; Vm: ventral median setae; Vl: ventral lateral setae.

floodwater and organic material during the rainy seasons. In general, the specimens have been collected in total darkness, where they actively roam across silt banks or walk on the walls or between karst formations (Rowland & Reddell 1979; Cokendolpher & Reddell 1992). The objective of this work is to describe a new species of the genus *Protoschizomus* from a cave in Guerrero, which confirms that the distribution of the family extends from the north to south of Mexico along the Sierra Madre Oriental and westward through the Mexican Trans-Volcanic Belt to the states of Guerrero and Colima.

The specimens were collected manually and preserved in 80% ethanol. They were subsequently examined and measured with a Nikon SMZ645 stereoscopic microscope fitted with an ocular micrometer. The measurements are given in mm, following Cokendolpher & Reddell (1992). The female spermathecae were dissected in 80% ethanol and cleared in lactophenol for 10 min (Krantz & Walter 2009), after which they were fixed in Hoyer's liquid, mounted in a permanent preparation, and examined with an optical microscope Nikon Eclipse E100. The male chelicerae were dissected in ethanol and observed in a semi-permanent preparation. The male flagellum and palp were suspended in 96% gel alcohol (to position firmly and prevent movement at the moment the picture is taken), and then were covered with a thin layer of liquid ethanol (80%) to minimize light diffraction during photography. We took photographs with a Nikon Coolpix S10 VR camera equipped with a microscope adapter and



Figures 9–11.—*Protoschizomus franckei* new species. Male holotype. 9. Right pedipalp, ectal view. 10. Right chelicera, ectal view. Female paratype. 11. Spermathecae. Scale bars: 0.2 mm (Figs. 9, 10), 0.05 mm (Fig. 11).

then edited the photographs with Adobe Photoshop CS5. The specimens are deposited in the Colección Nacional de Arácnidos (CNAN), Instituto de Biología, Universidad Nacional Autónoma de México (UNAM).

TAXONOMY

Family Protoschizomidae Rowland 1975
Genus *Protoschizomus* Rowland 1975

Protoschizomus Rowland 1975:2.

Type species.—*Agastoschizomus pachypalpus* Rowland 1973 by original designation.

Protoschizomus franckei new species
Figs. 1–11

Type material.—MEXICO: *Guerrero*: holotype adult male, Cueva de Boca del Diablo, Acuitlapán, Municipio Taxco de Alarcón (18.59916°N, 99.54579°W, 1594 m), 21 April 2012, G. Contreras, J. Mendoza, R. Monjaraz, D. Ortíz (CNAN-T0384). Paratypes: 1 adult female, 1 immature, same data as holotype (CNAN-T0385).

Etymology.—This species is dedicated to Dr. Oscar Francke for his contributions to Mexican arachnology and for his support provided to the author.

Diagnosis.—A species belonging to the *pachypalpus* species-group with a conical flagellum in the male, rather than a globose flagellum; propelpidium with four pairs of dorsal setae; and sternites II–VII with two irregular rows of setae. Males can be distinguished by the conical shape of the flagellum, ending in a triangular projection (Figs. 3–5); longer and narrower than that of *P. occidentalis* Rowland 1975; by the presence of two rows of setae, with five and three setae on the patella and five spinose setae on tibia (Fig. 9), in comparison to *P. occidentalis* which has three setae on the patella and four on the tibia, respectively.

Description.—*Male (holotype):* Pale brownish. Length, from anterior margin of propeltidium to base of flagellum 4.56 (Figs. 1, 2). *Prosoma*: Propeltidium 1.22 long, 0.60 wide; anterior process curved downward; with row of two setae on anterior process and one pair setae at base of proeess; with four pairs of dorsal setae, the second pair longer than the others and the last pair missing; without ocular spots. Mesopeltidial plates 0.26 long; gap between the plates 0.12. Metapeltidium divided, each plate 0.34 wide. Anterior sternum with 10 setae plus two sternopophysial setae; posterior sternum with four setae.

Chelicera: Serrula with eight teeth. Setae 1=3, 2=4, 3=9, 4=2, 5=0, 6=1 (Fig. 10).

Palp: Trochanter not produced distally, semi-ovate, without sharp distal margins and without mesal spur. Femur with four long, spiniform setae ventrally and four prolaterally. Patella ventrally with two rows of spiniform setae; mesal row with five setae, ectal row with three spiniform setae, basal shortest and distal longest. Tibia with three ventrolateral rows of spiniform setae, two mesal and one ectal, first mesal row with five setae, second mesal row with five setae and ectal row with five setae (Fig. 9). Basitarsus-tarsus with two symmetrical spurs 0.14 long; claw 1.22 long (Fig. 9).

Legs: Leg I, including coxa, 5.61 long; basitarsal-tarsal proportions: 23: 5: 6: 6: 6: 5: 21. Femur IV 4.2 times longer than deep.

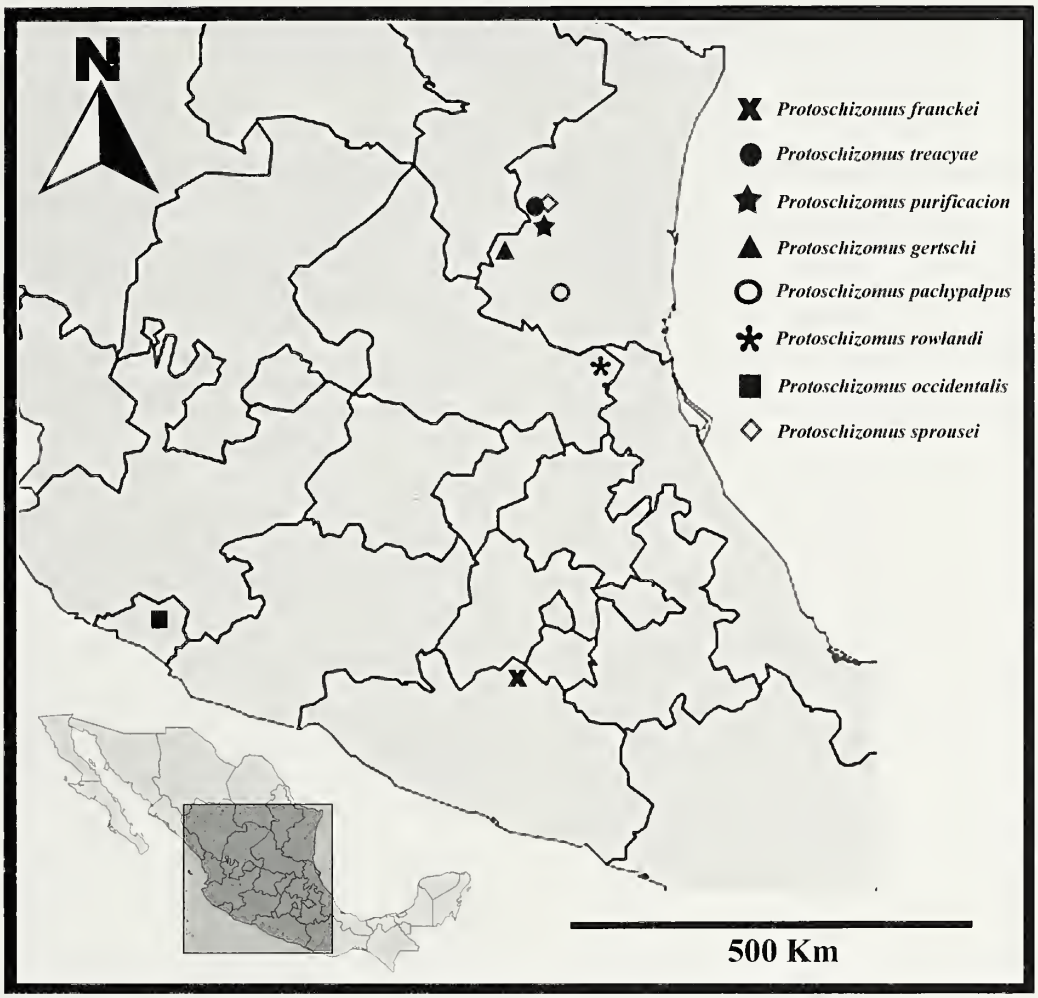


Figure 12.—Distributional records of the genus *Protoschizomus* Rowland 1975 in Mexico.

Opisthosoma: Tergite I with four anterior microsetae (in a row) and two large posterior setae; tergite II with six anterior microsetae (in a row) and two large posterior setae; tergites III–V and VII with two dorsal and two dorsolateral setae each; tergite VI with five setae, three dorsal and two dorsolateral setae; tergite VIII with two dorsal, four dorsolateral setae (in a row) and two lateral setae; tergite IX with two dorsal and two lateral setae; tergites X–XII semi-telescopic, XII being longest. Sternites II–VII with two irregular rows of setae near posterior margin; sternites VIII–IX with one row of setae; sternite X with one irregular row of setae; Genital plate clearly sclerotized. Sternite VI 3.5 times wider than long; width/length ratio versus body length, 1.2. Flagellum (Figs. 3–5) 0.64 long, 0.27 wide; conical, gradually expanded distally, with ventrolateral bulbs; seta dm2 absent.

Female (paratype): Similar to the male, differences: length from anterior margin of propeltidium to base of flagellum, 3.92. Propeltidium 1.48 long, 0.70 wide; setation as on male. Tergite setation as on male, except tergite VIII with two rows of setae on anterior and posterior margins, with five setae each. Sternite setation as on male, except on sternites VII and IX with two dorsal setae and four dorsolateral setae each; Sternite VI 3.6 times wider than long; width/length ratio versus body length, 1.08. Flagellum (Figs. 6–8) 0.60 long; dm2 setae absent; segments/articles I, III–V present. Spermathecae (Fig. 11) with one pair of short, tubular lobes not increasing in diameter apically; with two sclerotized plates behind the lobes. Chelicera: serrula with seven teeth. Setae 1=3, 2=4, 3=11, 4=2, 5=0, 6=1. Leg 1, including coxa, 5.24 long; basitarsal-tarsal proportions 17: 5: 5: 4: 5: 6: 20. Femur IV 3.4 times longer than deep.

Variation.—The male is larger than the female. The male pedipalps are longer and wider than on female. The number of teeth on the serrula of the chelicerae is eight in male and seven in female. Cheliceral setation: G3 varies, with nine on male and 11 on female.

Measurements (mm).—Male holotype (Female paratype): Pedipalp: trochanter 0.49 (0.42); femur 0.73 (0.68); patella 0.70 (0.64); tibia 0.67 (0.56); basitarsus-tarsus 0.30 (0.30); total 2.89 (2.60). Leg I: coxa 0.52 (0.44); trochanter 0.34 (0.34); femur 1.34 (1.10); patella 1.40 (1.28); tibia 1.26 (1.10); basitarsus 0.46 (0.27); tarsus 0.75 (0.71); total 5.61 (5.24). Leg IV: trochanter 0.60 (0.62); femur 1.28 (1.24); patella 0.64 (0.58); tibia 0.96 (0.90); basitarsus 0.84 (0.84); tarsus 0.62 (0.60); total 4.94 (4.78).

Distribution.—This species is known only from the type locality in the state of Guerrero (Fig. 12).

Related species.—*Protoschizomus franckei* resembles *P. occidentalis* Rowland 1975, from Colima, in that the male flagellum is broadly joined at the base, and seta vm4 is present; but they differ in size; *P. franckei* is larger (4.56) than *P. occidentalis* (4.00). The flagellum is narrower and longer in *P. franckei* than in *P. occidentalis* (Cokendolpher and Reddell 1992; Figs. 52, 53). The proportion of

pedipalp length versus body length is 0.63 for *P. franckei*, whereas for *P. occidentalis* it is 0.69. The number of spiniform setae varies from one species to the other: on the patella *P. franckei* has two rows of setae, with five and three setae, whereas on *P. occidentalis* it possesses only three setae; the tibia has three rows of setae, the ectal row with five setae, and on *P. occidentalis* it has only four setae. The spur is smaller (0.14) and the claw is bigger (1.22) in *P. franckei* than in *P. occidentalis* (0.3 and 0.6 respectively). The serrula has eight teeth on *P. franckei*, whereas *P. occidentalis* has seven; the number of setae varies throughout the chelicera. The propeltidium on *P. franckei* has one pair of setae less than on *P. occidentalis*.

Natural history.—We collected the specimens in a karstic cave, under a big rock, approximately 40 m from the entrance. The cave presents a considerable accumulation of mud on the ground and walls, indicating that it is subjected to periodic flash floods in the rainy season. The cave shows a high degree of human disturbance. The habitat outside the cave is deciduous oak forest.

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LITERATURE CITED

Cokendolpher, J.C. & J.R. Reddell. 1992. Revision of the Protoschizomidae (Arachnida: Schizomida) with notes on the phylogeny of the order. Texas Memorial Museum Speleological Monographs 3:31–74.

Harvey, M.S. 2003. Catalogue of the smaller arachnid orders of the World: Amblypygi, Uropygi, Schizomida, Palpigradi, Ricinulei and Solifugae. CSIRO Publishing. Collingwood Victoria, Australia.

Krantz, G.W. & D.E. Walter. 2009. Collecting, rearing, and preparing specimens. Pp. 83–96. *In* A Manual of Acarology. Third edition. (G.W. Krantz & D.E. Walter, eds.). Texas Tech University Press, Lubbock, Texas.

Lazcano, C. 1983. México paraíso de la espeleología. Gaceta UNAM, VI época 1(41):21.

Montaño-Moreno, H. & O.F. Francke. 2009. A new species of *Agastoschizomus* (Schizomida: Protoschizomidae) from Guerrero, Mexico. Texas Memorial Museum Speleological Monographs, Studies on the Cave and Endogean Fauna of North America 5(7):33–36.

Rowland, J.M. 1971. *Agastochizomus lucifer*, a new genus and species of cavernicole schizomid (Arachnida, Schizomida) from Mexico. Bulletin of the Association for Mexican Cave Studies 4:13–17.

Rowland, J.M. & J.R. Reddell. 1979. The order Schizomida (Arachnida) in the New World. I. Protoschizomidae and dumitrescoae group (Schizomidae: Schizomus). Journal of Arachnology 6:161–196.

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Carico, J.E. 1993. Trechaleidae: a "new" American spider family. Pp. 305. *In* Proceedings of the Ninth International Congress of Arachnology, Panama 1983. (W.G. Eberhard, Y.D. Lubin & B.C. Robinson, eds.). Smithsonian Institution Press, Washington, D.C.

Huber, B.A. & W.G. Eberhard. 1997. Courtship, copulation, and genital mechanics in *Physocyclus globosus* (Araneae, Pholcidae). Canadian Journal of Zoology 74:905–918.

Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66. *In* Spider Communication: Mechanisms and Ecological Significance. (P.N. Witt & J.S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

Platnick, N.I. 2011. The World Spider Catalog, Version 12.0. American Museum of Natural History, New York. Online at http://research.amnh.org/iz/spiders/catalog/

Roewer, C.F. 1954. Katalog der Araneae, Volume 2a. Institut Royal des Sciences Naturelles de Belgique, Bruxelles.

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